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Empirical Estimates of Carbon Production for a Meiobenthic Harpacticoid Copepod[1]

ROBERT J. FELLER

Department of Biology, The Marine Science Program and Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, SC 29208, USA

FELLER, R. J. 1982. Empirical estimates of carbon production for a meiobenthic harpacticoid copepod. Can. J. Fish. Aquat. Sci. 39: 1435–1443.

The intertidal harpacticoid copepod *Huntemannia jadensis* was sampled at approximately weekly intervals with five replicate cores at mean lower low water stations on three similar sand beaches in Puget Sound, Washington, from 1973 to 1974. Quantitative estimates of abundance of each developmental stage and direct measures of body carbon were used to calculate secondary production by two methods, one of which required knowledge of development times. Population biomass varied fivefold during the year. Production ranged from 0.75 to 1.75 mg $C \cdot 10\ cm^{-2} \cdot yr^{-1}$, varying with study area and computation method. Confidence intervals about single production estimates were extremely high, and 95% confidence limits about annual production estimates were 0.2–14.7 mg $C \cdot 10\ cm^{-2} \cdot yr^{-1}$. Turnover ratios for this harpacticoid were about 4 per year, low in comparison with other meiofaunal species. Eggs and naupliar growth accounted for ~50% of total annual production.

Key words: meiobenthos, secondary production, harpacticoid copepod, carbon, P/B ratio, Puget Sound

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De 1973 à 1974, on a prélevé des échantillons du copépode harpacticoïde intertidal *Huntemannia jadensis* à intervalles d'environ une semaine, retirant cinq carottes se répliquant à des stations de plus basse marée moyenne sur trois plages sablonneuses identiques du Puget Sound (Washington). Nous avons utilisé des estimations quantitatives d'abondance à chaque stade de développement et des mesures directes du carbone du corps dans le calcul de la production secondaire, et ce, d'après deux méthodes, dont l'une nécessitait une connaissance des temps de développement. Dans le cours de l'année, la biomasse de la population varie d'un facteur cinq. La production est comprise entre 0,75 et 1,75 mg $C \cdot 10\ cm^{-2} \cdot an^{-1}$, selon l'aire étudiée et la méthode de calcul. Les intervalles de confiance d'estimations uniques de

[1]Contribution No. 1269, Department of Oceanography, University of Washington, Seattle, WA 98195, USA, and contribution No. 456, Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, SC 29208, USA.

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production sont très larges, et les limites de confiance à 95 % pour les estimations de production annuelle sont de 0,2 à 14,7 mg $C \cdot 10\ cm^{-2} \cdot an^{-1}$. Les rapports de renouvellement de cet harpacticoïde sont d'environ 4 par année, ce qui est faible par comparaison avec les autres espèces méiofauniques. Les œufs et la croissance des nauplii sont responsables d'environ 50 % de la production annuelle totale.

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PAST production estimates for benthic meiofauna have relied upon indirect methodologies which use knowledge of the turnover rate of populations. McIntyre (1964) estimated the production of subtidal meiobenthos as between 2.5 and 3.8 g $C \cdot m^{-2} \cdot yr^{-1}$ by assuming a turnover rate of biomass (production:biomass or P/B ratio) of 10 per year. Gerlach (1971), in reviewing the probable energetic importance of meiofauna, estimated that meiofauna in general have a P/B ratio of 9 per year, or about five times the macrofauna ratio. But for a meiobenthic nematode, Gerlach (1972) estimated an annual P/B ratio of 26 per year, an order of magnitude higher than that for macrobenthos. For deep-sea meiofauna, Thiel (1975) assumed an average generation time of 1 yr for all taxa and estimated meiofaunal production to be in the range $0.005-0.05$ g $C \cdot m^{-2} \cdot yr^{-1}$, a value approximately one order of magnitude lower than deep-sea macrofauna production estimates. Ankar and Elmgren (1976) estimated meiofaunal production in shallow Baltic Sea stations as 2.7 g $C \cdot m^{-2} \cdot yr^{-1}$, with 20% due to harpacticoid copepods. Total benthic production for the Baltic stations was ~8.5 g $C \cdot m^{-2} \cdot yr^{-1}$.

Other workers have relied upon estimates of net growth efficiency to convert respiration measurements for various meiofaunal taxa to production (Dye et al. 1978; Warwick and Price 1979; Warwick et al. 1979). Teare (1978) also relied upon conversion of respiration by the harpacticoid *Tachidius discipes* to estimate production and failed to measure biomass directly. Production of four common harpacticoids from a brackish-water pond, including *T. discipes*, was estimated as $20-112$ mg $C \cdot m^{-2} \cdot yr^{-1}$ by assuming young copepodites equal one-eighth their adult weight and double in weight with each molt (Heip 1980). Zaika and Makarova (1979) provide simplified equations for computing specific production [mass (mass × area × time)$^{-1}$] using data on biomass, age structure, and field temperature for meiofaunal populations, but such data will rarely be available. Recently Fleeger and Palmer (1982) estimated production for *Microarthridion littorale*, a numerically dominant mud-dwelling harpacticoid in the southeastern United States. Data on population abundance were combined with biomass determinations of frozen individuals and independently derived specific growth rates from laboratory populations at various temperatures. By assuming its growth followed the von Bertalanffy form, Fleeger and Palmer (1982) estimated dry weight production for this small species in 1979 as ~15 $\mu g \cdot 10\ cm^{-2} \cdot yr^{-1}$, or about 6 mg $C \cdot m^{-2} \cdot yr^{-1}$ (if carbon equals 40% of dry weight).

In describing the life history and population dynamics of the numerically dominant harpacticoid copepod on intertidal sand beaches in Puget Sound, Washington, I found that *Huntemannia jadensis* had one generation per year in recognizable cohorts and could be reared in the laboratory (Feller 1977, 1980a, b). This species was thus an ideal choice to provide a direct estimate of carbon production for a mieofaunal species using quantitative empirical data from a natural field population. The methods used in this study were selected for their theoretical applicability to populations in which reproductive recruitment occurs during relatively short time intervals rather than continuously.

Materials and Methods

TARGET POPULATION

Complete details of sampling are given in Feller (1980a). In brief, 10-cm^2 cores were taken at stations along intertidal transects of three similar beaches in central Puget Sound at ~10-d intervals for at least 1 yr. A central zero tide level (mean lower low water, MLLW) station was sampled intensively with five replicate cores per visit. Core samples were decanted through a 73-μm mesh to retain all developmental stages of *H. jadensis*, including nauplii. Nauplii could not be accurately staged during enumeration and were thus lumped into a single naupliar category. All copepodite stages were identified and counted.

BIOMASS DETERMINATIONS

Animals were collected live in the field by scooping surface sand into a collection jar containing seawater. Collecting jars were held less than 10 d at 12°C before animals were sorted from the sediment. Animals could not be combusted directly after sorting, for most were usually covered with detritus, attached benthic diatoms, or parasites, which had to be removed before analysis. Therefore, sorted animals were placed into shallow Petri dishes containing filtered (0.45 μm) seawater and sand for 24 h at 12°C. The sand was from the same area where animals were collected and had been rinsed in distilled water, combusted at 450°C for 6 h, and rinsed again. This procedure allowed the animals to clear their intestinal tracts and to scrape themselves free of attached material by movement in the sand.

The copepods were next passed individually through two containers of distilled water to remove salts. The animals were then sorted to stage onto glass fiber filters for drying at 55°C for at least 24 h. After drying to constant weight, the animals were transferred to silver combustion chambers and stored in a desiccator until carbon analysis. Egg sacs were removed from gravid females, rinsed in distilled water, and placed into combustion chambers separately.

Biomass of the developmental stages of *H. jadensis* was measured as body carbon with an elemental analyzer (Carlo Erba, model 1100). In the range of $2-1000$ μg C, its stated accuracy is within about 1%. Eight developmental stages were combusted for carbon determinations: eggs, nauplii,

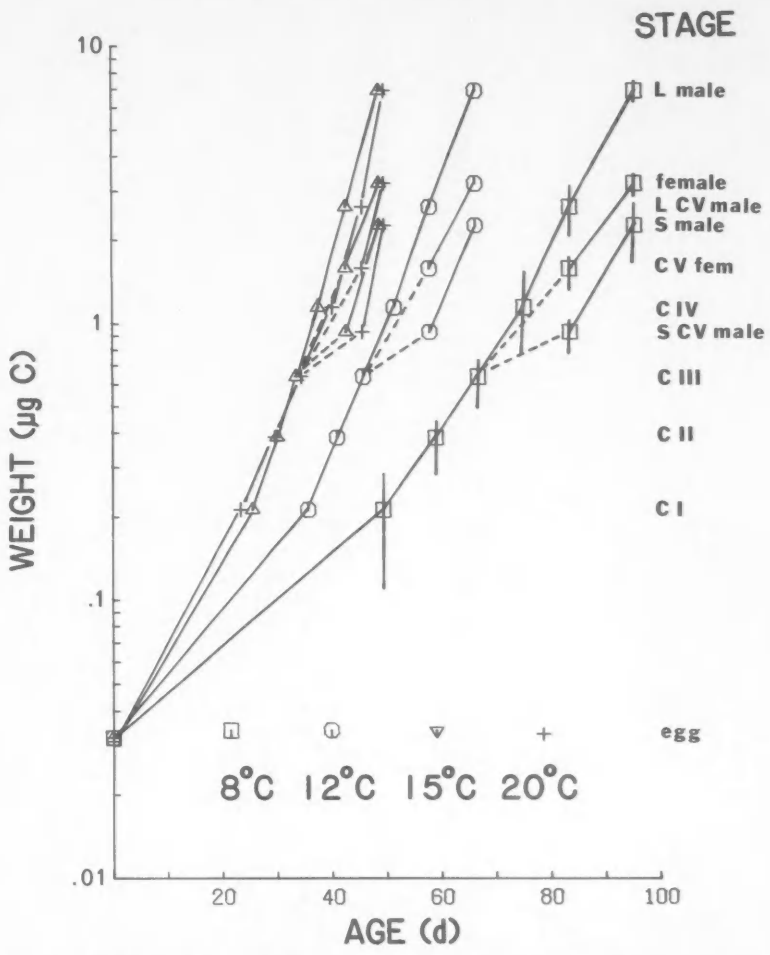

FIG. 1. Growth curves for copepodite stages of *H. jadensis* derived from laboratory estimates of development times at 8, 12, 15, and 20°C (see Feller 1980b). Sexual differentiation first occurs in the C IV stage, and males are dimorphic (L = large; S = small). Vertical bars are 95% confidence limits about individual body carbon weights.

C I–IV, C V male, and C V female. Initial egg weight was assumed to be zero, so the growth of adult females was simply the biomass of eggs they produced. Spermatophore production was neglected. The carbon content of an average nauplius was interpolated from a graph of body carbon per stage similar to Fig. 1. Biomass for each stage i on a given sampling date was calculated as the product of the geometric mean number of individuals per unit area (f_i) of a stage and its empirically determined carbon weight ($\overline{W}_i$).

SECONDARY PRODUCTION CALCULATIONS

One type of productivity calculation followed that of Crisp (1971) where summation of the type

$$P = \sum_{t=0}^{t=1} \sum_{i=0}^{i=n} f_i G_i \overline{W}_i \Delta t$$

applies to the number (f_i) of individuals of developmental stage i whose instantaneous growth rate (G_i) has been measured independently. Specific growth rates for each stage were calculated as

$$G_i = \frac{\ln \overline{W}_{i+1} - \ln \overline{W}_i}{\Delta t},$$

where $\overline{W}_i$ is body carbon and Δt is the developmental time of stage i in laboratory cultures taken from Feller (1980b, table

TABLE 1. Equations describing calculation of secondary production variability.

Two-level nested ANOVA:

(1) $X_{ijk} = \mu_{..} + \alpha_i + \beta_{ij} + e_{ijk}$.

Variance about daily biomass estimates:

(2) $V(B_i) = \overline{W}_i^2 V(N_i) + N_i^2 V(\overline{W}_i) + 2\overline{W}_i N_i \mathrm{cov}(\overline{W}_i, N_i)$.

Variance about average biomass between sampling periods:

(3) $V(\bar{B}) = 0.25\,[V(B_t) + V(B_{t+1}) + 2\mathrm{cov}(B_t, B_{t+1})]$, where $\bar{B} = (B_t + B_{t+1})/2$.

Variance about instantaneous growth coefficients:

(4) $V(G) = \sum^{k} G^2 - \left(\sum^{k} G\right)^2 \Big/ k \Big/ k(k-1)$.

Variance about a production estimate:

(5) $V(G\bar{B}) = G^2 V(\bar{B}) + \bar{B}^2 V(G) + 2G\bar{B}\mathrm{cov}(G, \bar{B})$,

where $\mathrm{cov}(G, \bar{B}) = r[V(G)V(B)]^{1/2}$.

Approximate 95% confidence limits about a production estimate:

(6) $P \times$ or $\div$ by antilog $(t_{0.05,\,df}[V(G\bar{B})/n]^{1/2}$.

B = population biomass (μg C·10 cm^{-2})
G = instantaneous carbon-specific growth rate (d^{-1})
k = number of replicate estimates of G
n = number of estimates of P during interval of interest
N_i = geometric mean number of individuals of the ith developmental stage per 10-cm^2 area
P = production during Δt (μg C·10 cm^{-2}·Δt^{-1})
r = correlation coefficient between G and $\bar{B}$
t = Student's t
W_i = body carbon weight of the ith stage
X_{ijk} = geometric mean abundance per 10 cm^2
$\mu_{..}$ = overall population mean
α_i = mean effect of weeks
β_{ij} = mean effect of sampling days within weeks
e_{ijk} = random error term

II) using linear interpolation to correct for average field temperatures on the dates of sample collections. The underlying assumption for calculating development times was that growth under excess food in the laboratory occurred at rates comparable to those of field populations in a fluctuating temperature regime (see Feller 1980b for discussion). Only body carbon values and development times measured for individuals from a given study site were used to calculate G_i's for that site; i.e. all calculations were site-specific.

Secondary production was also calculated by the mean weight–survivorship (Allen curve) method which assumes no particular growth function (Allen 1951). Estimates by this method are subject to error from fitting scattered data points. I connected data points with straight lines where possible and computed areas beneath straight-line segments of the curves. The instantaneous growth method of Crisp (1971) described above implicitly assumes exponential growth. Because the *H. jadensis* population was sampled at ~10-d intervals at each study area and there was but one collection of five replicate core samples on a given day, it was necessary to estimate the between-day variance of abundance which could then be applied in equations for calculation of production variance. The study period was divided into weekly intervals, many of which then contained more than one sampling date, i.e. several random observations within arbitrarily constructed weekly time intervals.

Estimation of between-day variance in abundance of each stage was from two-level nested analyses of variance (Eq. 1, Table 1) performed on $\log_{10}(N + 1)$ transformed counts for each of the eight separate developmental stages. The variance about body weights was estimated from logarithmically transformed carbon weights of individual stages combined for all three areas computed by a least squares ratio estimator (Sokal and Rohlf 1969). The variance about estimates of production by the instantaneous growth method was calculated according to Chapman (1968, 1978) using Eq. 2 through 6 (Table 1). Covariance terms in Eq. 2 and 3 were omitted because samples used to estimate weights and abundances were independent. Variance of an annual production estimate was the sum of the variances for all weekly estimates of production in that year.

Results

To avoid repetition, I will discuss in detail only the results from the Richmond Beach study area where the *H. jadensis* population developed one cohort during the year. Body carbon weights of similar developmental stages of *H. jadensis* were not the same at the three study areas (Table 2). As samples for these analyses were not collected concurrently, values for all areas were averaged to provide variance estimates which subsume this temporal variability. These average body carbon values show a clear exponential rate of increase over time (Fig. 1).

The biomass of *H. jadensis* was highest during summer and fall at mean lower low water stations with averages over all sampling dates of 231, 419, and 212 μg C·10 cm^{-2} at Mukilteo, Richmond Beach, and Golden Gardens, respectively (Fig. 2). These biomass curves generally conformed in shape with curves of population abundance over time except when large numbers of small nauplii predominated. Although the biomass at Richmond Beach was nearly twice as high as the other two sites, all three populations underwent about a fivefold change in biomass annually. Females and males accounted for most of the biomass present throughout the year. These observed biomasses were not all the result of production during the study period because many individuals initially present were produced in the previous generation. Biomass of these older individuals was excluded for computations of cohort production, and their exclusion reduced average biomass over the study period to 88, 215, and 132 μg C·10 cm^{-2} at the three respective study areas. Growth rates of *H. jadensis* in terms of carbon (μg C/d) generally increased with temperature with sometimes large differences among areas for a given temperature (Table 3).

After subtracting the biomass of individuals present before the start of the main cohort at Richmond Beach (cohort spanned Jan. 4–Sept. 19, 1974, 258 d), cohort pro-

TABLE 2. Mean weights (μg C per individual) and their 95% confidence limits for stages of *H. jadensis* collected at three study areas and averaged for all areas.

Stage[a]	Mukilteo		Richmond Beach		Golden Gardens		All areas	
	$\bar{x}$	(±)	$\bar{x}$	(±)	$\bar{x}$	(±)	$\bar{x}$	(±)
Egg	0.032	0.002	—	—	—	—	0.032	0.002
Nauplii	—	—	0.179	0.021	—	—	0.179	0.021
C I	0.191	0.093	0.264	—	0.218	—	0.213	0.122
C II	0.350	0.071	0.415	0.063	0.373	—	0.387	0.019
C III	0.580	0.094	0.689	0.114	0.537	0.996	0.642	0.026
C IV	1.109	0.382	1.484	0.335	1.098	1.777	1.147	0.293
C V female	1.246	0.101	1.883	0.804	1.547	—	1.580	0.151
Female	2.641	0.064	3.340	0.230	3.800	0.083	3.210	0.059
C V male (S)	0.923	0.055	0.983	—	—	—	0.934	0.033
C V male (L)	1.942	0.386	3.350	—	2.723	3.070	2.647	0.325
Male (S)	1.966	0.418	3.205	3.061	2.913	—	2.269	0.253
Male (L)	5.725	0.267	6.673	0.241	7.779	5.080	6.943	0.174

[a](S) = small morph, (L) = large morph.

duction by Crisp's method during the 359-d study period was 1.748 g C · 10 cm^{-2}, or about 1.75 g C · 10 $cm^{-2} \cdot yr^{-1}$. Confidence limits (95% level) about each single sampling interval for which production was calculated were quite variable, ranging from a factor of 2 to 10 times the computed production value for the interval. Confidence limits for annual production were 0.2−14.7 g C · 10 $cm^{-2} \cdot yr^{-1}$, a factor of 8.4. Cohort production by the Allen curve method was 1.628 g C · 10 $cm^{-2} \cdot 359\ d^{-1}$ (Fig. 3).

Production estimates were about twice as high at Richmond Beach compared with the two other study areas, but the proportion of total production by each developmental stage of *H. jadensis* was quite similar at all three areas (Table 4). Egg production and growth of eggs through the naupliar stages accounted for 49.6−59% of total production, with growth of fifth-stage copepodites accounting for about 25% (Table 4). Annual production-to-biomass, or turnover ratios ranged from 3.25 to 4.17 if the average observed biomass values were used, and from 5.98 to 8.53 using only biomass actually produced by the cohort (Table 5).

Discussion

Of the several methods available for estimating secondary production of aquatic invertebrates (see Edmondson and Winberg 1971), all are subject to potential error because natural populations seldom conform with restrictions and assumptions implicit in any particular method. This is to be expected in populations with complicated life histories and complex growth patterns (Waters 1979). Errors in estimating the life span of a cohort can lead to serious under- and overestimation of production (Allen 1971), and even for populations with simple and clear life histories, no two methods applied to the same data appear to give the same result (Waters and Crawford 1973; Cushman et al. 1978). The major problems common to all methods concern our inability to sample the same target population repeatedly in a variable environment and in obtaining accurate and precise estimates of abundance and biomass over time (Resh 1979).

Differences between the levels of annual production by *H. jadensis* estimated by the Crisp (1971) and Allen (1951) curve methods were considerably less than the differences between the three study areas. Both methods resulted in estimates within about 10% of each other, but Richmond Beach production was twice that of the other two areas. This was due to the nearly twofold higher average biomass supported on that particular beach (Fig. 2). Although confidence limits about the instantaneous growth production estimates were high, such close agreement with the Allen curve method (and two others, see Feller 1977) instills confidence in the reliability of these estimates and the derived P/B ratios.

Many more estimates of secondary productivity by meiofaunal-sized organisms are needed before we can begin to assemble an overview of the energetic importance of these small metazoans. More discouraging, however, is the lack of variability estimates in other published studies of invertebrate production, as their absence makes it difficult if not impossible to compare results. For whatever reasons, even the editor of a major aquatic ecology journal has stated, "A completely quantitative study would provide confidence limits for biomass and production when these are estimated. Unfortunately, confidence limits are difficult to obtain; . . ." (Sutcliffe 1979). None of the secondary production studies cited in review articles by Mullin (1969), Conover (1974), or Crisp (1975) gives estimates of variability, although some probable ranges for their estimates are given. A notable exception is the study of production by a planktonic ctenophore in which variabilities associated with sampling error and spatiotemporal effects were estimated (Hirota 1974). The study by Fleeger and Palmer (1982) provides confidence limits about some of their estimates, but it is unclear whether they should be applied to production estimates for specific size-classes or only to estimates for specified time intervals for the whole population. If the latter is true, their variability was approximately an order of magnitude lower than that for *H. jadensis* in this study.

Harpacticoid copepod abundances are typically very much lower in North Inlet (South Carolina) than in Puget Sound (Feller 1977). This difference is made more evident in comparing production by the two species investigated by

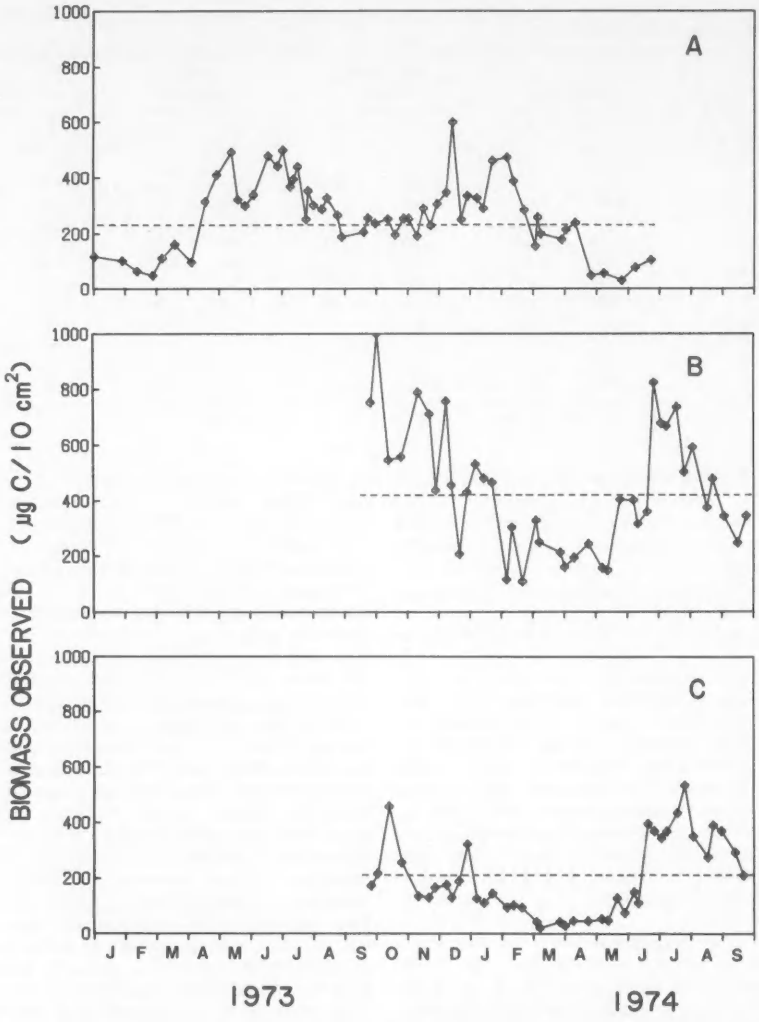

FIG. 2. Observed biomass of *H. jadensis* at mean lower low water (MLLW) stations of (A) Mukilteo, (B) Richmond Beach, and (C) Golden Gardens in Puget Sound, Washington. Broken line indicates average for the study period.

Fleeger and Palmer (1982) and by myself. Comparing the larger sand-dwelling *H. jadensis* with the smaller mud-dwelling *M. littorale*, adults weighed from 2 to 5 times more than *M. littorale* (as body carbon), were nearly two orders of magnitude more dense at peak abundance periods, produced two to three orders of magnitude more carbon per unit area per year, but turned over four times slower. Their three smallest size-classes (all nauplii) accounted for 39% of the total *M. littorale* production, and naupliar production by *H. jadensis* was about 35% of the total (Table 4). Contrary to the assertion by Heip (1980) that naupliar production for harpacticoids is negligible, the results of Fleeger and Palmer (1982) and my own suggest that the growth of naupliar forms may be a very significant portion of total production. Because Fleeger and Palmer (1982) did not estimate egg production, other studies will be required to confirm the results for *H. jadensis* (where egg production was about 20% of the total).

Daily production of *H. jadensis* ranged from about 1 to 4 μg $C \cdot 10\ cm^{-2} \cdot d^{-1}$ over the year, with peak values ap-

TABLE 3. Specific growth rates (μg C/d) for *H. jadensis* from three study areas under excess food as a function of temperature (°C). MK = Mukilteo, RB = Richmond Beach, GG = Golden Gardens.

Stage transition	Area	Temperature (°C)					
		10	11	12	13	14	15
Egg to nauplius	MK	0.113	0.119	0.124	0.138	0.152	0.165
	RB	0.163	0.171	0.178	0.197	0.217	0.236
	GG	0.162	0.170	0.177	0.197	0.215	0.236
Nauplius to C I	MK	0.019	0.020	0.022	0.025	0.028	0.032
	RB	0.013	0.014	0.015	0.017	0.019	0.021
	GG	0.006	0.007	0.008	0.009	0.010	0.011
C I to C II	MK	0.089	0.102	0.114	0.121	0.128	0.135
	RB	0.066	0.076	0.085	0.090	0.095	0.101
	GG	0.079	0.090	0.101	0.107	0.113	0.119
C II to C III	MK	0.086	0.096	0.105	0.123	0.136	0.144
	RB	0.087	0.097	0.106	0.119	0.132	0.145
	GG	0.062	0.069	0.076	0.085	0.094	0.104
C III to C IV	MK	0.095	0.104	0.114	0.130	0.146	0.162
	RB	0.113	0.124	0.135	0.154	0.173	0.192
	GG	0.105	0.115	0.125	0.143	0.161	0.179
C IV to C V male	MK	0.070	0.074	0.078	0.085	0.092	0.099
	RB	0.111	0.118	0.125	0.137	0.148	0.160
	GG	0.124	0.132	0.140	0.153	0.166	0.178
C IV to C V female	MK	0.016	0.017	0.018	0.020	0.022	0.023
	RB	0.033	0.035	0.037	0.040	0.043	0.047
	GG	0.047	0.050	0.053	0.058	0.062	0.067
C V male to adult	MK	0.108	0.117	0.127	0.143	0.159	0.175
	RB	0.058	0.063	0.068	0.077	0.085	0.094
	GG	0.107	0.116	0.125	0.140	0.156	0.172
C V female to adult	MK	0.077	0.084	0.089	0.100	0.111	0.123
	RB	0.070	0.076	0.082	0.092	0.102	0.113
	GG	0.091	0.099	0.107	0.120	0.133	0.147

TABLE 4. Annual production by Crisp method (μg C · 10 $cm^{-2} \cdot yr^{-1}$) of *H. jadensis* at three study areas; MK = Mukilteo, RB = Richmond Beach, GG = Golden Gardens.

Stage transition	MK		RB		GG	
	Prod.	%	Prod.	%	Prod.	%
Eggs	169	22.5	382	21.8	139	17.6
Eggs to nauplius	211	28.1	650	37.2	252	32.0
Nauplius to C I	12	1.5	46	2.6	4	0.5
C I to C II	22	2.9	49	2.8	5	0.7
C II to C III	33	4.4	53	3.0	10	1.2
C III to C IV	57	7.7	122	7.0	35	4.4
C IV to male C V	78	10.4	105	6.0	42	5.3
C IV to female C V	18	2.4	31	1.8	16	2.0
C V male to adult male	100	13.3	154	8.8	151	19.2
C V female to adult female	51	6.7	155	8.9	135	17.1
Total	751	100	1748	100	789	100

proaching 15 to 20 μg C · 10 $cm^{-2} \cdot d^{-1}$. Extrapolation from these peak values to an annual production figure would result in artificially high P/B ratios unrepresentative of actual annual turnover rates; nor would extrapolation to other areas of the results for *H. jadensis* at the single stations sampled at each of these three study areas be particularly wise, as these stations were within the strata of highest population abundance throughout the study period. Comparison with other studies of benthic or planktonic production is difficult for this reason and because of the many different methods and units used by other investigators. However, the few good studies completed indicate that production of *H. jadensis* is similar to that of many common planktonic herbivores in neritic waters (see table 1 in Mullin 1969; table 1 in Conover 1974). That *H. jadensis* can have a daily level of production similar to that of planktonic herbivores is rather surprising considering the relatively slow turnover rate of this small species. Comparison of *H. jadensis* annual production with that of macrobenthic organisms indicates that most have higher levels of standing stock and annual production than meiobenthos

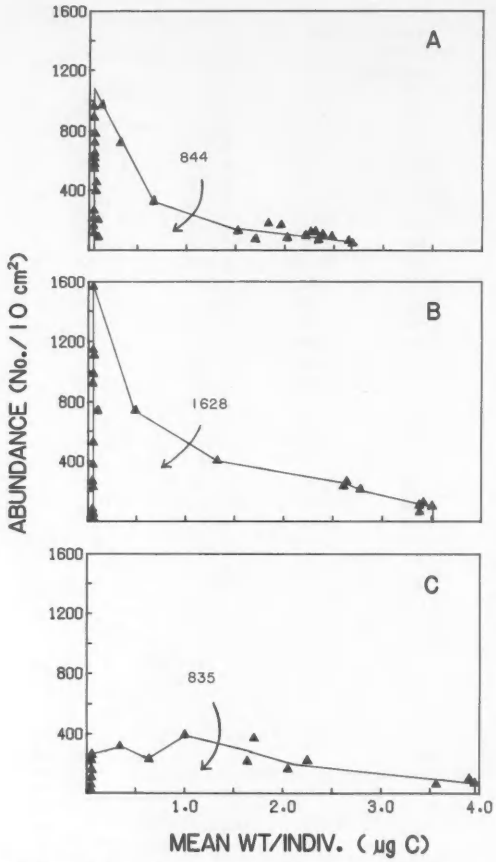

FIG. 3. Mean weight–survivorship (Allen) curves for calculating cohort production of *H. jadensis* at MLLW stations of (A) Mukilteo, (B) Richmond Beach, and (C) Golden Gardens in Puget Sound, Washington. Production estimate is integrated area under the curve as $\mu g\ C \cdot 10\ cm^{-2} \cdot yr^{-1}$.

(table 7 in Crisp 1975).

Because no two populations are alike, it is difficult to recommend a method for estimating secondary production of marine benthos. The turnover (P/B) ratio method of Waters (1969) is attractive for its simplicity and has also been used by many other investigators. Other methods require various levels of effort, but whatever method is selected, one should always try to estimate confidence limits for production estimates. Without them, comparisons are tentative, and at best, highly speculative. The recent paper by Krueger and Martin (1980) describing computational methods for constructing confidence intervals in the size–frequency method of estimating secondary production is a welcome addition to the literature.

Mullin (1969) advocated abandonment of the holistic approach in estimating secondary production of entire communities or groups of functionally similar organisms growing and dying at different rates. Single dominant species should be investigated separately before syntheses for entire communities are attempted. The fallacy of assuming that all organisms having similar trophic dependencies (e.g. herbivores and carnivores) or which are of similar size will have similar turnover rates (see also Banse and Mosher 1980) becomes evident in current food web models of large ecosystems (e.g. Mills and Fournier 1979). Also, Warwick (1980) cautions that knowledge of production for a few dominant species, each with different specialized trophic behavior, is not likely to provide reliable estimates of production for entire communities. Warwick further cautions that P/B ratios are unreliable at the species level but may be all right to use at community levels. Estimates of secondary production, then, must be interpreted judiciously.

Huntemannia jadensis, being large and growing slowly, may not be energetically representative of the 2500 or so other species of harpacticoid copepods described, nor are there many regions in the marine benthic environment dominated by harpacticoids. But if one assumes that this intertidal species having just one generation per year is representative of other meiobenthic taxa, the combined production of several taxa having more than one generation per year will be appreciably higher than the $1\ g\ C \cdot m^{-2} \cdot yr^{-1}$ level of production I have estimated for this single species. Such levels could easily exert an even higher energetic demand on organic matter input to the benthic environment than envisioned by Steele (1974). The actual demand will depend on the magnitude of biomass present and other factors as well, but studies of harpacticoid assimilation efficiency indicate that these organisms have gross growth efficiencies comparable to those of planktonic copepods, further indicating the potential importance of meiofauna in benthic ecosystems.

TABLE 5. Production to biomass (P/B) ratios (yr^{-1}) for *H. jadensis* at three study areas.

Comments	Mukilteo	Richmond Beach	Golden Gardens
Crisp method	3.25[a]	4.17[a]	3.72[a]
	8.53[b]	8.13[b]	5.98[b]
Allen curve	3.78[a]	3.89[a]	3.94[a]
	9.59[b]	7.57[b]	6.33[b]

[a]Using average biomass observed as denominator.
[b]Using average cohort biomass as denominator.

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Model of Salmon Age Structure and Its Use in Preseason Forecasting and Studies of Marine Survival

RANDALL M. PETERMAN

Department of Biological Sciences and Natural Resources Management Program, Simon Fraser University, Burnaby, B.C. V5A 1S6

PETERMAN, R. M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444 – 1452.

A method is derived to determine whether ocean abundance of a salmon stock affects either the survival rate between particular ages or the proportion of the ocean population which migrates back to freshwater spawning areas. The approach, similar to Fredin's smolt indices method, uses data on brood-year contributions to adult returns in successive years. Survival rate and proportion maturing are found to be independent of stock abundance after age 3, except in Naknek River sockeye (*Oncorhynchus nerka*) data. In cases such as Babine Lake sockeye salmon, where nonlinearity has been identified previously in the relation between smolt abundance and total adult returns, this lack of density dependence in the older ages means that the mortality processes which cause that nonlinearity act early in smolt life. The relations between abundance of adult returns of age n in year t and returns of age $n+1$ from the same brood class in year $t+1$ are useful as preseason forecasting techniques. The method derived here, which uses logarithms of abundances, improves upon the existing forecasting method. Deviations from the relation between abundances of brood-year returns can in some cases be explained by smolt weight, which is shown to affect mean age at return.

Key words: salmon age structure, marine survival, age-at-return, smolt weight, preseason forecasting

PETERMAN, R. M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444 – 1452.

Une méthode a été mise au point pour déterminer si l'abondance en mer d'un stock de saumons influence soit le taux de survie entre âges particuliers, soit la proportion de la population en mer qui retourne vers les frayères en eau douce. Tout comme dans la méthode des indices de smolts de Fredin, on a utilisé les contributions des diverses classes d'âge au nombre des adultes qui reviennent en des années successives. On a constaté que le taux de survie et la proportion de sujets en voie de maturation sont indépendants de l'importance du stock après l'âge 3, sauf dans le cas du saumon nerka (*Oncorhynchus nerka*) de la rivière Naknek. Dans des cas comme celui du saumon nerka du lac Babine, où l'on avait déjà observé l'absence de linéarité dans la relation entre l'abondance des smolts et le nombre total des adultes retournant en eau douce, cette absence de dépendance de la densité chez les groupes plus âgés signifie que les processus de mortalité responsables de cette non-linéarité agissent tôt dans la vie des smolts. Comme méthodes de prédiction avant la saison, les relations entre l'abondance des adultes retournant à l'âge n dans l'année t et les retours de saumons d'âge $n+1$ de la même classe d'âge dans l'année $t+1$ sont utiles. La méthode décrite dans le présent article, utilisant les logarithmes d'abondance, marque un progrès sur la méthode de prédiction existante. On peut, dans certains cas, expliquer les déviations de la relation entre l'abondance des retours d'une classe d'âge par le poids des smolts, qui influence l'âge moyen du retour en eau douce.

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IN another paper (Peterman 1982), I incorporated data on sampling errors of smolt abundance estimates into an analysis of marine survival rates and showed that for Babine Lake sockeye salmon (*Oncorhynchus nerka*), the best-fit relation between brood-year smolt and adult abundances is nonlinear, contrary to expectations. This nonlinearity was attributed to (1) density-dependent marine survival, (2) highly variable survival processes that tend to mask the underlying relation between smolts and adults, or (3) a combination of (1) and (2). In that paper, calculations were made of the magnitude of smolt enumeration errors below which one would conclude

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that other salmon populations such as Bristol Bay sockeye salmon and Oregon coho salmon (*O. kisutch*) also have nonlinear relations between smolts and adults. In the present paper, I describe the methodology which was developed to pinpoint the specific segments of the smolt-to-adult life stage in which most of these density-dependent or highly variable mortality processes operate. This is done by utilizing information on abundance of total adult returns, at different ages, from a given cohort of smolts. This paper covers the method referred to in Peterman (1982) as unpublished data.

Several management agencies currently use linear fits between untransformed abundances of salmon returns of age n in year t and returns of age $n+1$ in year $t+1$ as preseason forecasting methods (Alaska Department of Fish and Game 1981; Gunsolus 1978; R. Kadowaki, Canada Department of Fisheries and Oceans, Prince Rupert, B.C., personal communication). For example, age 5 returns in 1980 are predicted from age 4 returns in 1979. In the case of Oregon coho, Gunsolus (1978) fits a linear model to untransformed data for jack returns and adult returns in the following year, and interprets it as an indication that marine survival is not density dependent between those ages. Yet on the basis of other analyses, Gunsolus argues, density-dependent mortality appears to occur sometime in the total smolt-to-adult period. Combined with the above interpretation of the linear jack-to-adult relation, Gunsolus deduces that the density dependence must occur between time of seaward migration of smolts and return of jacks. Though these conclusions seem reasonable, they are not justified for coho salmon, or any other species, until it is shown (1) that the data for the jack-to-adult period are not significantly nonlinear, and (2) that linear relations between abundances of successive aged returns from a given brood class actually reflect density-independent mortality. The present paper derives a formal model to test these ideas on several salmon populations.

Numerous methods exist to estimate survival rates of salmon through various portions of their marine life by using data on marking experiments, high seas catches, and smolt abundances compared with adult returns (e.g. Fredin 1964, 1965; Lander 1973; Mathews 1968; Mathews and Buckley 1974; Parker 1960, 1962; Ricker 1962, 1976). None of these models has been directly used to determine whether marine survival at any particular stage is related to salmon abundance. In this paper, I derive a method similar to Fredin's (1965) smolt indices method. It differs from Fredin's model in that it allows survival and proportion of the ocean population maturing at a given age to be dependent on density of that stock. By doing so the model permits a test of the possibility that survival and proportion maturing are density dependent. In addition, I assume a multiplicative error term instead of an additive one as used by Fredin because it has been shown (Peterman 1981) that the former type of term is more consistent with data from the marine life stage of salmon than the latter. As is described below, a multiplicative error term permits simple estimation of the appropriate parameters to test for linearity and density independence.

Methods

Data Sources

Full descriptions of data for Babine Lake sockeye and for coho salmon in the Oregon Production Index area are found in Peterman (1982) and Gunsolus (1978), and they are not repeated here. Only three Bristol Bay sockeye populations are examined here, Kvichak River, Naknek River, and Ugashik River, and data cover through return year 1980. Total returns (catch and escapements), by age and stock are from summary data sheets provided by K. Parker and C. Meacham (Alaska Department of Fish and Game, Anchorage, AK, personal communication), which are based on a series of Technical Data Reports published for each year's returns (e.g. Meacham and Nelson 1980). Catch estimates are based on fish sales slips, and escapements are based on visual counts from towers. The fish scales used to derive age structure are sampled from catches and escapements. Mixed stock catches in terminal areas are apportioned to appropriate rivers based on the comparison of age–sex composition in catches with that in the escapements (McCurdy and Schroeder 1972). Japanese high seas catches are allocated to stocks, by age, in proportion to the relative total returns to each river system by age. The former allocation method is unlikely to bias the analysis consistently in any direction but the latter may do so if high seas fishing is selective for some stocks. Within each stock, different freshwater-age smolts (sub-2 or sub-3) are treated as separate groups for the purposes of the data analyses. The Alaska Department of Fish and Game refers to sub-2 fish as resulting from age I smolts and sub-3 fish as age II, but the Gilbert–Rich notation is used here (e.g. 5_2 and 5_3). Annual average smolt weights are from Meacham (1981) as well as the summary data sheets of K. Parker and C. Meacham described above.

Model

British Columbia and Alaskan sockeye that are categorized as sub-2's by the Gilbert–Rich system (i.e. that spend two winters in freshwater during the egg-to-smolt stage) exhibit the following general pattern of marine events. Smolts are enumerated in freshwater during their downstream migration and they enter salt water, say for simplicity, June 1 of their 2nd year. About 14 mo later the first adults return as age 3_2 fish. Fish remaining in the ocean are exposed to mortality and a portion of the population which remains at the end of the next 12-mo period migrates back toward freshwater at age 4_2. This process is repeated until the total cohort of smolts is depleted (usually with age 5_2 for B.C. sockeye, and 6_2 for some Alaskan stocks, although small numbers of older ages occasionally appear). Similar events occur for fish smolting as sub-3's, except the first adults return at age 4_3. This conceptual framework for a single cohort can be formalized using the following notation, where all abundance symbols represent numbers of fish at different ages, from the same brood class. Subscripts on letter symbols refer to the nearest total maturity age since spawning, and the example chosen is for the age 3-to-4 stage.

X_3 = abundance of fish in ocean just prior to return migration of age 3 fish (R_3)

O_3 = abundance of fish in ocean just after return migration of age 3 fish

R_3 = abundance of age 3 returns (catch plus escapement)

h = a parameter in the equation relating O_3 to X_4, to allow for density dependence of s_3

TABLE 1. Rounded statistics for the relations $Y = a + bX$ shown in Fig. 1–6 between natural logarithms of abundance (in millions) of age n adult returns in year t and age $n+1$ returns in year $t+1$. Functional or geometric mean regression statistics are given except for Babine Lake sockeye 3_2-4_2, where a predictive regression is also shown in parentheses because 3_2 fish are accurately enumerated at a counting fence. P values show the probability that the observed result could be drawn from a population in which the indicated null hypothesis is true. (*Significant at $\alpha = 0.05$, or less.)

Stock	Age stanza	Sample size, yr	a	b	s_b	$P_{b=1}$	r	$P_{r=0}$	r^2
Kvichak R. sockeye	3_2-4_2	10	7.461	1.232	0.321	>0.4	0.68	<0.05*	0.46
	4_2-5_2	24	−0.759	0.889	0.096	>0.2	0.86	<0.001*	0.74
	4_3-5_3	18	4.520	0.846	0.116	>0.2	0.84	<0.001*	0.71
	5_3-6_3	23	−1.550	0.812	0.114	>0.1	0.76	<0.001*	0.58
Naknek R. sockeye	3_2-4_2	15	3.766	0.716	0.172	>0.1	0.50	=0.057	0.25
	4_2-5_2	24	0.333	0.721	0.124	<0.05*	0.59	<0.01*	0.35
	4_3-5_3	19	3.208	0.725	0.131	=0.051	0.66	<0.01*	0.44
	5_3-6_3	24	−0.214	0.549	0.107	<0.001*	0.40	=0.0504	0.16
Ugashik R. sockeye	3_2-4_2	9	6.667	1.116	0.282	>0.5	0.74	<0.05*	0.55
	4_2-5_2	24	−0.082	0.97	0.081	>0.5	0.92	<0.001*	0.85
	4_3-5_3	14	3.791	0.794	0.146	>0.1	0.77	<0.01*	0.59
	5_3-6_3	24	−1.10	1.039	0.159	>0.5	0.70	<0.001*	0.49
Babine L. sockeye	3_2-4_2	15	1.52 (1.20)	0.914 (0.763)	0.139	>0.5 (>0.1)	0.84	<0.001*	0.71
	4_2-5_2	22	0.084	1.204	0.23	>0.2	0.53	<0.01*	0.28
Oregon coho	2_2-3_2	15	2.825	0.916	0.075	>0.1	0.96	<0.001*	0.92

m_3 = proportion of X_3 that migrates back toward freshwater at age 3

s_3 = proportion of exponentiated abundance of O_3 which survives to X_4

X_4 = abundance of fish in ocean just prior to return migration of age 4 fish (R_4)

g = a parameter in the equation relating X_4 to R_4, to allow for density dependence of m_4

O_4 = abundance of fish in ocean just after return migration of age 4 fish

R_4 = abundance of age 4 returns (catch plus escapement)

m_4 = proportion of exponentiated abundance of X_4 that migrates back toward freshwater at age 4

e = base of natural logarithms

v,w = normally distributed random error terms each with mean zero.

The example below is derived for the age 3-to-4 stage of a cohort of smolts that enters the ocean at age 2. Similar formulae are easily derived for other stages and other smolt types (sub-3's).

(1) $R_3 = m_3 X_3$

or

(2) $X_3 = R_3/m_3$

(3) $O_3 = (1 - m_3)X_3$

By allowing for survival rate to vary with abundance and adding a multiplicative, lognormal error term as argued for by Allen (1973), Walters (1975), and Peterman (1978, 1981),

(4) $X_4 = s_3 O_3^h e^v$

Now, allowing for proportion maturing at age 4 to vary with abundance and adding a noise term,

(5) $R_4 = m_4 X_4^g e^w$

Substitute equations (2)–(4) into (5) and obtain

$$\begin{aligned} R_4 &= m_4(s_3 O_3^h e^v)^g e^w \\ &= m_4 s_3^g O_3^{gh} e^{gv} e^w \\ &= m_4 s_3^g [(1 - m_3)X_3]^{gh} e^{gv+w} \end{aligned}$$

(6) $R_4 = m_4 s_3^g [(1 - m_3)R_3/m_3]^{gh} e^{gv+w}$

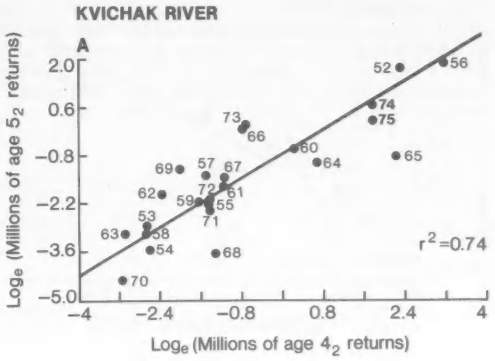
Taking natural logarithms,

$$\log_e R_4 = \log_e m_4 + g \log_e s_3 + gh \log_e[(1 - m_3)R_3/m_3] + (gv + w)$$

(7) $$\log_e R_4 = \log_e m_4 + g \log_e s_3 + gh \log_e [(1 - m_3)/m_3] + gh \log_e R_3 + (gv + w)$$

This is a linear relation between $\log_e R_4$ and $\log_e R_3$, with slope $b = gh$ and an intercept, a, equal to the first three constant terms on the right side of equation 7. To determine if survival rate or proportion maturing varies with abundance, the null hypotheses that $h = 1$ and $g = 1$ should be tested. Failure to reject those null hypotheses means there is no evidence that survival and maturation rate are density dependent. However, these two null hypotheses cannot be tested separately by comparing the slope of the $\log_e - \log_e$ regression to 1.0, using a two-tailed t-test. Such a comparison only tests the null hypothesis that the product $gh = 1$. It is possible that either g or h is > 1 and the other parameter is < 1, and that the two balance out so that the product $gh = 1$. However, such exact compensation between the two density-dependent processes is unlikely, as is discussed later. Therefore, if the t-test fails to reject the null hypothesis that $gh = 1$, this probably indicates that neither survival nor maturation rate is density dependent. It also indicates there is no significant nonlinearity in the relation between abundances of successive-aged returns from the same brood.

As noted by Ricker (1973, 1976), the parameter estimates



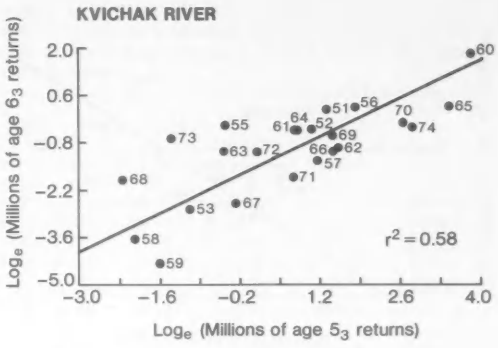
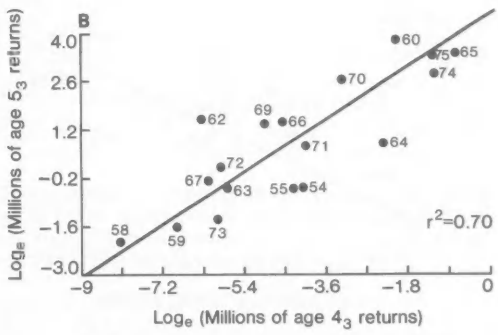


FIG. 2. Same as Fig. 1 except for age 5_3–6_3 relation.



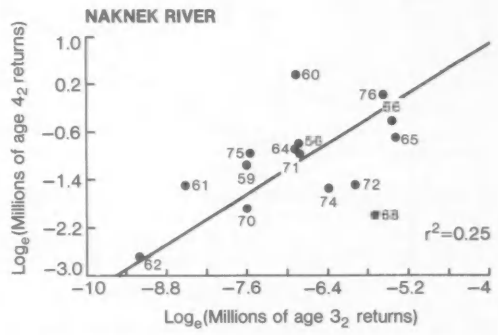


FIG. 1. Relation between abundances of age 4 returns of Kvichak River sockeye salmon in a given year and age 5 returns in the following year. Abundances are expressed as millions of fish, and brood years are denoted beside points. See Table 1 for equations. (A) 4_2–5_2 relation, (B) 4_3–5_3 relation.

FIG. 3. Relation between abundances of age 3_2 returns of Naknek River sockeye salmon in a given year and age 4_2 returns in the following year. Abundances are expressed as millions of fish, and brood years are denoted beside points. Table 1 gives the equation.

for equation (7) are best derived from a functional or geometric mean regression because both R_3 and R_4 are subject to considerable measurement error.

The general form of equation (7), which can be used between other ages, is

$$\log_e R_n = \log_e m_n + g \log_e s_{n-1} + gh \log_e [(1 - m_{n-1})/m_{n-1}] + gh \log_e R_{n-1} + (gv + w) \quad (8)$$

where n is age of the older age-class in the analysis.

There are several assumptions in this approach to testing for density dependence between successive ages. First, the exponents in the error terms, v and w, must be normally distributed and independent. Data on independence are lacking, but Peterman (1981) documents the normality condition for v, and similar central limit theorem principles probably apply to w as well, because w is a product of a sequence of events affecting growth and migration of fish. As g is a constant, the product gv is also normally distributed, as is the sum $gv + w$. Second, variation in abundance estimates around true values creates no difficulty, as this is absorbed by the error term in equation (8). However, any consistent bias in those estimates will increase the likelihood of rejecting the null hypothesis of linearity. Such biases might potentially arise from such factors as noncatch losses from fishing where the loss rate is a function of fish abundance or from density-dependent predation during the return migration to freshwater. It is assumed here that such biases are small and the findings described in the Results section tend to support this view. As will be seen, the null hypothesis of linearity is rejected in only a few cases, so few that those cases may be due to chance alone. If consistent biases of the type described above are present in the data, they must be small in magnitude because the data fit the assumed model closely. Finally, the proportion of fish maturing at the earliest age in each analysis is assumed to be independent of density. Significant departures from this assumption would reduce the power of the above test for $gh = 1$.

PRESEASON FORECASTING

The model derived above has additional application, to the management problem of predicting salmon-run sizes from previous years' data. A preseason forecasting method presently used by management agencies, already mentioned in the

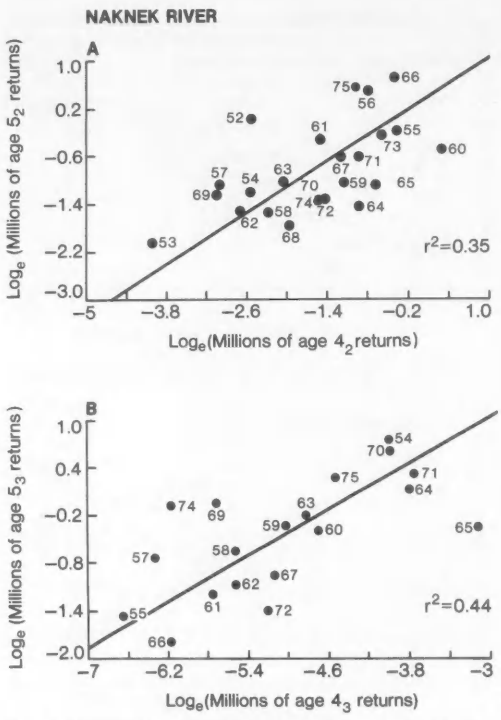


FIG. 4. Same as Fig. 1 except for Naknek River sockeye. (A) 4_2-5_2 relation, (B) 4_3-5_3 relation.

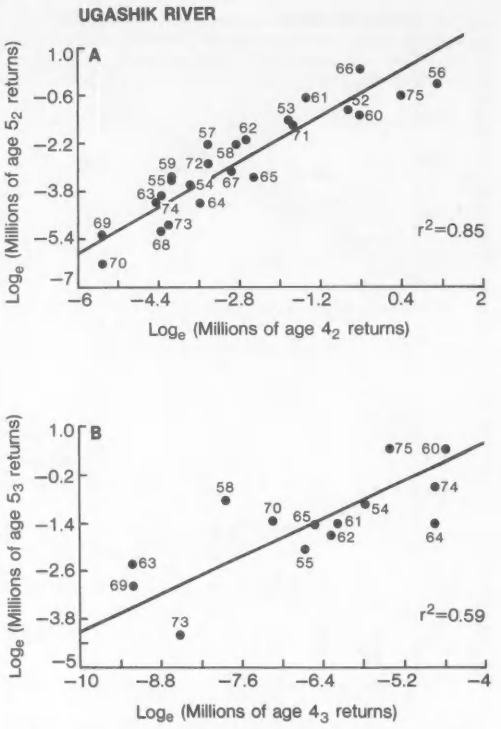


FIG. 5. Same as Fig. 1 except for Ugashik River sockeye. (A) 4_2-5_2 relation, (B) 4_3-5_3 relation.

introduction, calculates a linear regression using untransformed abundance estimates to predict age $n+1$ returns in year $t+1$ from age n returns in year t. But the model derived here uses logarithms of those abundances to fit linear relations, in accordance with equation (8). The mean square errors about the regression lines for these two different methods are not directly comparable, because in the first case the residual in additive form is in millions of fish, and in the second model the additive residual is in $\log_e$ (millions of fish). However, by definition, the method which best meets the assumptions of linear regression parameter estimation will give the best predictions. Therefore, the "untransformed" and "logarithmic" plot methods are compared by empirically testing how well each method meets two of the standard linear regression assumptions. Specifically, (1) Y-variates should be normally distributed at each X value and (2) samples should be homoscedastic, i.e. the variance around the regression line should be constant and independent of the value of X.

These tests are performed by the methods described in detail in Peterman (1981). The null hypothesis (H_0) of homoscedasticity is tested for each of the "untransformed" and "logarithmic" plot methods by calculating, for each set of stock data, Kendall's (1955) τ_b statistic of rank correlation between the absolute value of residuals from the regression line and their associated X values. Then the null hypothesis of

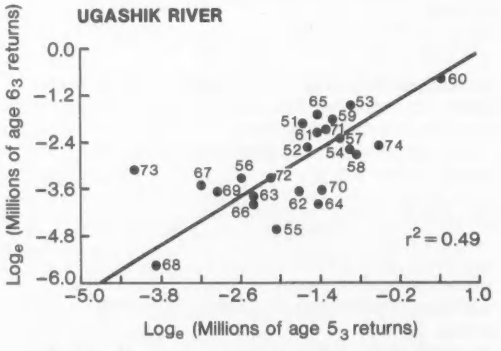


FIG. 6. Same as Fig. 5 except for age 5_3-6_3 relation.

normally distributed residuals is tested by using the Anderson–Darling statistic A^2 (Stephens 1974) to compare the frequency distribution of residuals with the expected normal one.

As above, results are tabulated for the functional regression estimates of the regression line, for both the "untransformed"

TABLE 2. Results of tests for homoscedasticity and normality of residuals for the presently used preseason forecasting method ("untransformed") and the method represented by equation (8) ("logarithmic"). See text for explanation. For the homoscedasticity test, H_0 = no association between absolute value of residuals and value of X variate. For the normality test, H_0 = residuals drawn from a normal distribution, and P values are from Stephens' (1974), Table 2. (*Significant at $\alpha = 0.05$, or less.)

			Homoscedasticity test				Normality test			
			"Untransformed"		"Logarithmic"		"Untransformed"		"Logarithmic"	
Stock	Age stanza	Sample size	τ_b	P	τ_b	P	A^2	P	A^2	P
Kvichak	3_2-4_2	10	0.33	>0.2	−0.29	>0.2	0.47	>0.15	0.21	>0.15
	4_2-5_2	24	0.50	<0.001*	0.01	>0.9	3.14	<0.01*	0.40	>0.15
	4_3-5_3	18	0.44	<0.05*	0.09	>0.6	1.99	<0.01*	0.20	>0.15
	5_3-6_3	23	0.49	<0.001*	−0.20	>0.1	1.34	<0.01*	0.58	>0.10
Naknek	3_2-4_2	15	0.39	<0.05*	0.22	>0.2	0.88	<0.025*	0.24	>0.15
	4_2-5_2	24	0.46	<0.01*	0.14	>0.3	1.00	<0.01*	0.25	>0.15
	4_3-5_3	19	0.18	>0.20	−0.06	>0.7	1.18	<0.01*	0.20	>0.15
	5_3-6_3	24	0.44	<0.01*	0.09	>0.5	0.95	<0.025*	0.54	>0.10
Ugashik	3_2-4_2	9	0.44	>0.10	−0.28	>0.3	1.09	<0.01*	0.26	>0.15
	4_2-5_2	24	0.27	=0.07	0.15	>0.3	3.81	<0.01*	0.86	<0.025*
	4_3-5_3	14	0.21	>0.30	−0.16	>0.4	1.33	<0.01*	0.18	>0.15
	5_3-6_3	24	0.47	<0.01*	−0.07	>0.6	0.21	>0.15	0.31	>0.15
Babine	3_2-4_2	15	0.35	=0.07	0.05	>0.8	0.33	>0.15	0.29	>0.15
	4_2-5_2	22	0.11	>0.50	−0.25	>0.1	0.30	>0.15	0.19	>0.15
Oregon	2_2-3_2	15	0.64	<0.001*	0.30	>0.1	0.64	=0.075	0.96	<0.01*

and "logarithmic" plot methods because of the measurement error in the X variates (Ricker 1973). However, as will be seen, exactly the same general conclusions are reached if the predictive regression estimates are used.

EFFECT OF SMOLT WEIGHT

Other variables beside abundance may affect the proportion of fish maturing at a given age and hence may contribute variation to the relation given in equation (8). One of many possibilities is body size, which reflects growth rate, which in turn may be related to the trigger for return migrations (Foerster 1968). Data on body sizes of fish on the high seas have not been gathered regularly but data on smolt body sizes are available. Bilton (1971) hypothesized that fish entering salt water at a large body size are likely to mature at an earlier age than small smolts. This hypothesis is tested here by relating weighted mean age at return of a given brood class to mean smolt weight. Weighted mean age at return is calculated from relative abundance of returns (catch plus escapement) in each age-class, from a given smolt run. In addition, smolt weight is correlated with residuals from the relation, described by equation (8), between abundance of returns of successive ages in successive years.

Results

LINEARITY TEST

Table 1 shows that in 2 out of the 15 cases examined, the null hypothesis, $b = gh = 1$, can be rejected at the $\alpha = 0.05$ level of significance. No particular importance can be attached to these two cases since the probability of having 2 out of 15 cases significant at $\alpha = 0.05$ is 0.13 (Pearson and Hartley 1972). Furthermore, the significant result for Naknek River age 5_3-6_3 fish is due solely to one extreme outlying data point. Note that a third case, Naknek River 4_3-5_3, is marginally above the significance level at $P = 0.0514$. Thus, the only cases close to rejecting the null hypothesis of linearity are in the Naknek River populations. Figures 1−6 illustrate some example relationships fit by equation (8); see Peterman (1982) for plots of the Babine Lake sockeye and Oregon coho cases.

PRESEASON FORECASTING

Table 2 indicates that the "untransformed" abundance fitting method presently used by management agencies for preseason forecasting is less appropriate than the "logarithmic" plot method derived here. This is because the latter method best meets the assumptions of the parameter estimation technique. The null hypothesis of homoscedasticity is rejected in 8 out of 15 cases for the "untransformed" plot approach and in no cases for the logarithmic plot method. For comparison, these values are 7/15 and 1/15, respectively, when predictive regression statistics are used. The increasing variance in Y values with increasing X for the "untransformed" cases are often clear simply by inspection, as depicted by the example in Fig. 7. The null hypothesis of normally distributed residuals around the regression line is rejected in 10 out of 15 cases for the "untransformed" plot method but in only 2 out of 15 for the "logarithmic" approach. Again, predictive regressions show the same trends, with rejections occurring in 9/15 and 1/15 cases, respectively. Although he did not explicitly state the implied models, Bilton (1973) found a similar improvement with logarithms in his study of catches of different-aged chum salmon (*O. keta*) in successive years.

In Table 1, 13 out of 15 cases show significant correlations

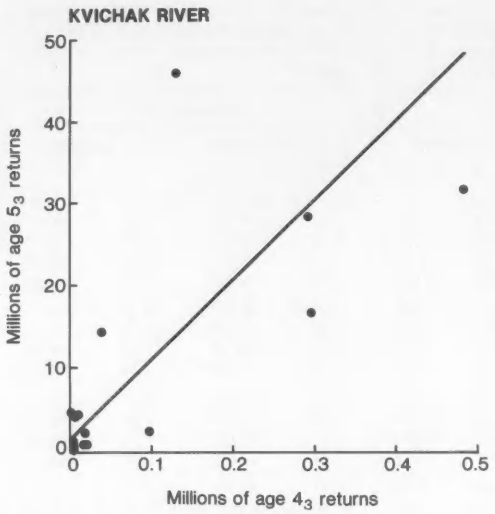


FIG. 7. Plot showing heteroscedasticity in relation between untransformed abundances of age 4_3 returns in year t and age 5_3 returns in year $t+1$, for Kvichak River sockeye salmon. Compare with Fig. 1B.

between abundances of successive aged returns in successive years ($P_{r=0} < 0.05$), and over half of these correlations account for more than 50% of the variability in the data.

EFFECT OF SMOLT WEIGHT ON AGE AT RETURN

Results in Table 3 show that Naknek River sockeye salmon is the only Bristol Bay stock examined which shows a significant relation between smolt weight and mean age of adult returns (Fig. 8A-B). Babine Lake sockeye, as discussed in Peterman (1982), also show this inverse trend ($r = -0.47$, $n = 18$, $P < 0.05$). In these significant cases, large smolts tend to return as adults at an earlier age than small smolts. Smolt weights are also significantly inversely correlated with residuals from the $\log_e - \log_e$ return relations derived from fitting equation (8), but only in the case of Naknek River sub-2 sockeye ($r = -0.65$, $n = 18$, $P < 0.01$) and Babine Lake sockeye ($r = -0.49$, $n = 18$, $P < 0.04$). In those cases, smolt weight data can improve the preseason forecasting methods discussed above by explaining some of the deviations in the $\log_e - \log_e$ relations.

Discussion

In 13 out of 15 cases, we cannot reject the null hypothesis that the product $gh = 1$. In those cases, therefore, there is no evidence for nonlinearity in the relation between adult returns of successive ages from the same brood. A value of g or h equal to 1 means that the proportion maturing or surviving, respectively, is not related to density. In order for gh to equal 1, both parameters must be 1, or another situation must exist: if either the survival or maturation rate decreases with abundance, then the other factor has to increase accordingly. For example, if survival of age 3's, s_3, decreases with increasing abundance, O_3, then this must be exactly compensated for by m_4, the proportion returning at age 4, increasing with O_3. This is an unlikely situation as lower survival is usually associated with smaller fish (Ricker 1962, 1976) and these fish would most likely mature later than usual, at age 5. Additional arguments apply to the oldest significant age of maturation, where less variability is possible in maturation rate in order to compensate for density-dependent survival changes. For example, adults of Babine Lake sockeye salmon rarely mature

TABLE 3. Correlations between mean smolt weight and weighted mean age of adult returns for the entire brood class.

Stock	Sample size, yr	r	$P_{r=0}$
Kvichak R. sockeye			
sub-2's	16	−0.06	>0.9
sub-3's	16	0.08	>0.9
Naknek R. sockeye			
sub-2's	18	−0.82	<0.001
sub-3's	18	−0.49	<0.04
Ugashik R. sockeye			
sub-2's	15	−0.07	>0.9
sub-3's	15	0.20	>0.9

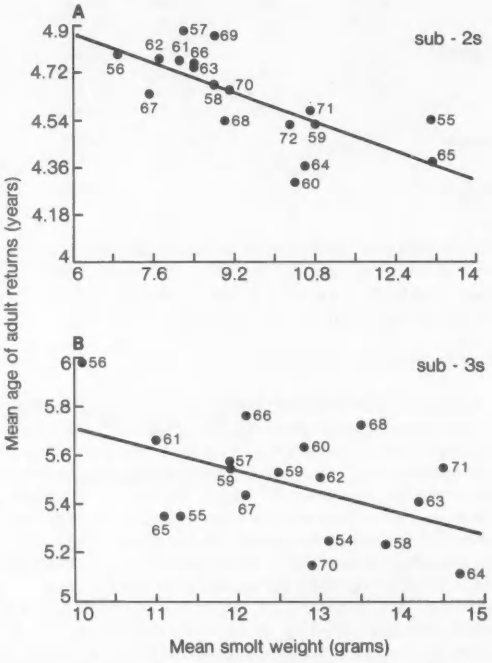


FIG. 8. Mean age of adult returns for Naknek River sockeye salmon as a function of smolt weight, by brood year. (A) sub-2 fish, (B) sub-3 fish.

at ages older than 5. Therefore m_5, the proportion of the remaining ocean population of a given cohort which matures at age 5, is usually close to 1.0 and clearly cannot go above 1.0. Given this fact, the parameter g cannot be much larger than 1 when it expresses the density dependence of m for the oldest significant age for a population. Hence, if the product $gh = 1$, h must also be very close to 1.

Therefore, while we cannot separately identify the values of g and h, circumstantial evidence strongly suggests that both g and h are near 1 in those 13 cases where the null hypothesis $gh = 1$ cannot be rejected. The power of the linear regression test of H_0 $gh = 1$ may, at first glance, seem relatively low, but the high r values in Table 1 and lack of obvious nonlinearities in Fig. 1–6 suggest that this is not a serious problem.

A value of h near 1 means that survival through a particular age does not vary systematically with a stock's ocean abundance of that age-group. Based on results in Table 1, this conclusion is reached for Kvichak River, Ugashik River, and Babine Lake sockeye, and Oregon coho salmon. Therefore, if density-dependent marine survival is demonstrated to occur, by subsequent analyses, in the total smolt-to-adult life stage for one of these populations, then most of the density-dependent survival probably occurs at an earlier life stage than the ones tested in Table 1. Peterman (1982) presents an application of this reasoning. I document a nonlinear relation between smolt abundance and total adult returns for Babine Lake sockeye and, based on the method derived here, I conclude that most of the density-dependent or highly variable, relation-masking mortality occurs in the 15 mo between smolt migration and return of age 3 jacks. Further discussion of these early life mortality processes is given in Peterman (1982). Similar suggestions for density dependence in the early ocean period are made for Oregon coho salmon (Gunsolus 1978; Peterman 1982). The present analysis confirms Gunsolus' earlier interpretation of the linear relation between untransformed abundances of jacks and adults.

Because Naknek River sockeye comprise the only cases evaluated here in which the product gh even approaches differing from 1 significantly, one is prompted to ask if there is something unique about this stock that might lead to nonlinearity in the relations between abundances of returns. However, a review of literature on the biology of Bristol Bay sockeye salmon does not offer any clues. The timing and movement patterns of the Naknek River stock are quite similar to other Bristol Bay sockeye populations (Straty 1974). Although the Naknek River population is the only one in Bristol Bay that shows consistent relations between smolt weight and mean age of return as hypothesized by Bilton (1971), this cannot explain why $gh < 1$ for Naknek fish. This is because Babine Lake sockeye also show this same inverse relation between body size and mean age of return (Peterman 1982), yet for Babine Lake sockeye, the product gh does not differ significantly from 1.

The main values of the method derived here are (1) identification of age stanzas where nonlinear relations arise between abundances and (2) improved preseason forecasting through use of logarithms. The latter results clearly demonstrate the value of what should be standard practice, namely explicitly stating the model implied by a particular parameter estimation method and testing the required assumptions.

Acknowledgments

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Influence of Hatchery Experience on Growth and Behavior of Juvenile Atlantic Salmon (*Salmo salar*) Within Allopatric and Sympatric Stream Populations[1]

T. A. DICKSON[2] AND H. R. MACCRIMMON

Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1

DICKSON, T. A., AND H. R. MACCRIMMON. 1982. Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. Can. J. Fish. Aquat. Sci. 39: 1453–1458.

Hatchery-reared Atlantic salmon (*Salmo salar*), wild Atlantic salmon and brook trout (*Salvelinus fontinalis*) (0^+ year-class fish) were observed in allopatric or paired sympatric populations using stream tanks at the Matamek Research Station, Quebec. Hatchery-reared salmon maintained a position just off the substrate, a position intermediate to that occupied by wild salmon (bottom) and trout (midwater). Growth rates of hatchery-reared and wild salmon were not statistically different. Neither type had an interactive advantage. It is concluded that the behavioral pattern of hatchery-reared salmon was intermediate to that of wild salmon and trout. This behavioral shift may account for poor survival of planted Atlantic salmon juveniles, a phenomenon suggesting the need for a reexamination of present live release programs using juvenile hatchery-reared salmon.

Key words: behavior, hatchery-rearing effects, growth, interspecific interactions, stream tank study, juvenile Atlantic salmon, juvenile brook trout

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Des saumons atlantiques (*Salmo salar*) d'élevage et sauvages ainsi que des ombles de fontaine (*Salvelinus fontinalis*) sauvages (poissons de classe d'âge 0^+) ont été observés en populations allopatriques ou sympatriques paires dans des bassins en cours d'eau à la station de recherche Matamek, au Québec. Les saumons d'élevage maintiennent leur position juste au-dessus du substrat, une position intermédiaire entre celle occupée par les saumons sauvages (au fond) et par les ombles de fontaine (entre deux eaux). Il n'y a pas de différence significative de taux de croissance entre saumons d'élevage et sauvages. Aucun type n'a d'avantage interactif. Nous concluons que le comportement des saumons d'élevage est intermédiaire entre celui de saumons et ombles de fontaine sauvages. Ce glissement de comportement peut expliquer la faible survie de peuplements de jeunes saumons atlantiques, phénomène qui fait ressortir le besoin de réexaminer les programmes d'ensemencements par saumonneaux d'élevage.

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THE river release of juvenile hatchery-reared Atlantic salmon, *Salar salmo*, of wild parentage is a common management practice in eastern North America and Europe. There is evidence, however, that their survival is much lower than for wild fish (Harris 1973). Based on an extensive literature review, Elson (1975) estimated that 8–12% of released hatchery-reared underyearlings survived to age 1 in comparison to 38% for naturally produced fish.

Several studies have revealed behavioral differences between wild and hatchery-reared Atlantic salmon juveniles which may affect relative survival rates. For example, Symons (1969) demonstrated that, unlike wild fish, hatchery-reared juveniles did not respond to overcrowding by normal downstream migration when first planted in a stream. Also, Sosiak et al. (1979) observed that age 1 hatchery-reared salmon ate a less varied diet, and tended to hold a more off-bottom station than did wild fish.

In view of these findings, the present study examined the behavior, growth and interactions of juvenile hatchery-reared and wild Atlantic salmon under simulated natural environmental conditions, using the Matamek River (50°18′N; 65°57′W) as a water source. Because of the prevalence of

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[2]Present address: Environmental Management Associates, 1510 Tenth Avenue S.W., Calgary, Alta., T3C 0J5.

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sympatric populations of brook trout, *Salvelinus fontinalis*, and Atlantic salmon in the salmon rivers of eastern North America, our study has included an examination of both species in allopatric and sympatric situations.

Materials and Methods

The study was conducted at the Matamek Research Station of the Woods Hole Oceanographic Institution, near Sept Îles, Quebec. Wild salmon and brook trout juveniles used in the study were netted below the Second and Third Falls of the Matamek River, a sixth order stream draining a small watershed of 684 km^2 on the north shore of the Gulf of St. Lawrence. Hatchery-reared salmon, the progeny of the wild Matamek River adults, were reared at the Tadoussac Hatchery of the Quebec Government, and returned to the Research Station as alevins on July 5, 1979.

The experiments were conducted in three parallel flumes within a stream tank, using river water, at the Second Falls of the Matamek River (Gibson and Power 1975). The experimental fish were held in 1 m^2 mesh pens in the downstream end of the flumes. Supplies of wild salmon and trout were captured throughout the summer and also kept in this manner. Each flume was also divided into three sections (60 × 150 cm) by vexar screening (3.2 mm mesh) with six fish placed in each section. The bottom was covered with a sand and gravel mixture to a depth of 10 cm. Water depth was maintained at 30.0 (± 1.0) cm, and water velocity at 14–22 $cm \cdot s^{-1}$. Observations of the test populations were made through the glass wall of each flume from a dark chamber.

Six 14-d trials were conducted between July 6 and September 28, 1979. Test populations consisted of wild salmon, hatchery-reared salmon, or brook trout studied separately (i.e. in allopatry), or pairs of the three in combination (i.e. in sympatry). Before each experiment, the fish were anesthetized with CO_2 (produced by 'Alka-Selzer' tablets placed in water), individually marked by hot branding the caudal fin (McNichol and Noakes 1979), weighed (Sartorius #3704, ± 0.01 g), and measured to the nearest mm (fork length). Fish of approximately the same size were used in each test.

Food was introduced at the upstream end of each flume section each evening at a rate of 1.0 $g \cdot fish^{-1} \cdot d^{-1}$, and drifted downstream with the current. The food, *Pandalus borealis*, had been boiled, ground up and reduced to a slurry by blending with water. Trials were ended by removing the fish and repeating the weighing and measuring procedure. The next trial was started immediately. Fish up to 5.0 cm were re-used in successive trials.

Behavioral observations were made on 10 occasions throughout each 14-d trial. At the beginning of each observation period, the horizontal and vertical position of each fish was recorded. For the next 15 min, successive agonistic acts resulting in displacement were documented (Gibson 1977), and the subordinate and dominant fish were noted (Brown 1975). All observations were recorded on a portable tape recorder, and later transcribed to data sheets. This procedure was then repeated for each of the other eight flume sections. Behavioral displays were "charge and chase," "approach," "drift," "nip," "lateral display," "frontal display," "presence," and "supplant" (Gibson 1977).

Growth of individual fish was measured as percent increase per day. The prevalence of each of the eight behavioral displays was expressed as a percentage of all displays. Significant variation in growth and behavior caused by the treatment (population mixes) was analyzed using a statistical program package (2V, BMDP, Jennrich and Sampson 1977). The model was a one factor completely randomized block design with blocking on replicates (Steel and Torrie 1960). As equal samples were required, the number of data points in each population was reduced to equal numbers with the aid of a random number table, as were the duplicate populations in each trial (Jennrich and Sampson 1977). Each F ratio was tested at $P < 0.1$ and $P < 0.05$.

Behavioral changes relative to treatments were identified by: the average distance to nearest neighbor (measured from the map plots made each observation), average number of interactions per individual, percent wins by each species in the sympatric populations, and the number of individual interactions won by dominant and subordinant wild salmon, hatchery-reared salmon or trout. All behavior and growth data for the Atlantic salmon types and the brook trout within each experimental population were averaged. Duplicate populations in each trial were averaged, and these means then averaged for each experiment by population type for non-statistical comparisons.

Results

We observed that juvenile wild salmon held station in the medium or fast current in contact with the substrate, using their pectoral fins as diving planes to maintain position. By contrast, the trout generally resided midwater or near the surface in medium or slow current. Hatchery-reared salmon held position just off the bottom of the stream tank, thus maintaining a vertical position intermediate to that of the wild salmon and trout. This positioning by hatchery-reared salmon did not appear to change seasonally during the experimental period.

Apart from vertical positioning, wild salmon, hatchery-reared salmon, and trout all used the same repertoire of behavioral displays in allopatry or sympatry but to considerably different extents (Table 1). Neither the percentage use of each behavioral display, nor the use of the behavioral displays in the different population mixes (allopatry or sympatry) varied significantly (at 90 or 95% levels) between the hatchery-reared and wild salmon. However, there was a tendency, but not to a significant extent, for wild salmon to use less "lateral display" than hatchery-reared salmon (Table 1).

In general, other than "supplant" which neither species used, the percentage use of each of the behavioral displays by the brook trout differed from that of both salmon types. The trout varied significantly ($P < 0.05$) from the salmon in the use of "approach" and "frontal display" while salmon used a significantly ($P < 0.1$) different proportion of "charge and chase." When in sympatry with trout, wild and hatchery-reared salmon showed a significant ($P < 0.05$) increase in the use of "approach" (Table 1).

In the allopatric populations versus the mixed populations the growth (percent increase $\cdot fish^{-1} \cdot d^{-1}$) in both fork length and weight varied significantly only at the following levels; wild salmon — fork length α = 50% and weight α = 50%,

TABLE 1. Percentage use of each behavioral display (averaged by population mix) by juvenile salmon (hatchery and wild) and trout, and averages ($\bar{x}$) for each species or type, in the Matamek stream tank, 1979.

Population type[a]	Charge and Chase	Approach	Drift	Nip	Lateral display	Frontal display	Presence
Salmon wild							
alone	42.9	4.9	0	43.5	7.3	0	0.9
mixed/T	41.1−	13.3	0	37.9	6.0	0	1.8
mixed/Sh	40.0−	8.5	0	40.8	8.7	0	2.0
($\bar{x}$)	(41.3)	(8.5)	(0)	(40.7)	(7.3)	(0)	(1.6)
Salmon hatchery							
alone	39.4	5.6	0	42.0	12.4	0	0.7
mixed/T	36.2−	10.4	0.2	38.4	12.9	0	2.0
mixed/Sw	42.2	4.8	0	41.7	9.4	0	2.0
($\bar{x}$)	(39.3)	(6.9)	(0.1)	(40.7)	(11.6)	(0)	(1.6)
Trout							
alone	24.4	29.0	0	36.8	9.1	1.8	0.6
mixed/Sw	22.5−	27.5−	1.3+	39.3+	7.1−	0.7−	0.7+
mixed/Sh	19.7−	34.3+	0	34.4−	8.6−	2.4+	1.2+
($\bar{x}$)	(22.2)	(30.3)	(0.4)	(36.8)	(8.3)	(3.7)	(0.8)

[a] T, Trout; Sh, Salmon hatchery; Sw, Salmon wild.

TABLE 2. Measurements of growth and behavior (with standard deviation) from the Matamek stream tank, 1979.

Population type[a]	n[b]	Starting fork length (cm)	Average percent increase · fish^{-1} · d^{-1}		Average distance to nearest neighbor (cm)	Average number of interactions · individuals^{-1} · trial^{-1}[c]
			Fork length (cm)	Weight (g)		
Salmon wild						
alone	54	4.1 (±0.5)	0.8 (±0.5)	3.5 (±2.8)	36.7 (±3.6)	8 (±4.3)
mixed/T	27	4.1 (±0.5)	0.8 (±0.4)	4.1 (±2.9)	38.1 (±4.5)	8 (±6.5)
mixed/Sh	21	4.5 (±0.3)	0.6 (±0.4)	2.5 (±2.5)	33.5 (±1.9)	12 (±4.0)
Salmon hatchery						
alone	54	4.3 (±0.2)	0.7 (±0.3)	3.6 (±1.4)	37.2 (±5.0)	6 (±3.4)
mixed/T	22	4.3 (±0.3)	0.8 (±0.4)	4.1 (±2.0)	37.8 (±5.8)	14 (±7.9)
mixed/Sw	21	4.3 (±0.3)	0.6 (±0.3)	3.4 (±2.3)	37.5 (±2.7)	12 (±9.9)
Trout						
alone	66	4.4 (±0.3)	0.6 (±0.4)	3.2 (±2.8)	31.7 (±3.8)	30 (±6.5)
mixed/Sh	27	4.3 (±0.3)	0.7 (±0.5)	3.4 (±2.8)	22.5 (±6.0)	12 (±7.9)
mixed/Sw	27	4.1 (±0.6)	0.7 (±0.5)	3.6 (±3.5)	26.3 (±3.3)	9 (±7.8)

[a] T, Trout; Sh, Salmon hatchery; Sw, Salmon wild.
[b] Number of fish observed.
[c] Only trials 2–6.

hatchery-reared salmon — fork length α = 10% and weight α = 25%, and trout — fork length α = 50% and weight α = 50%. However, the average gains in weight (and to a lesser extent, length) for each type of salmon and for the trout, within the three possible population mixes for each, did vary, although not at a significant level (Table 2). When trout were in sympatry with either wild or hatchery-reared salmon, or vice-versa (either salmon type in sympatry with trout), there was a greater average gain in weight per fish than when the salmon or trout were in allopatry. This pattern also showed up somewhat in daily increases in fork length. With population mixes of wild and hatchery-reared salmon, however, both types showed a lower daily gain in weight (and length) than when alone (Table 2).

When the allopatric populations (only) of the wild salmon, hatchery-reared salmon and trout were statistically analyzed, there was a significant seasonal variation (α = 95%) for both weight and fork length. While the growth in fork length of wild salmon (all population types) varied seasonally (α = 90%), and while there was a significant seasonal variation in the growth in weight of hatchery-reared salmon (α = 95%), there was no significant seasonal variation in the use of the eight behavioral displays.

The average distance to nearest neighbor was similar ($\geq$ 37 cm) for wild or hatchery-reared salmon in all population mixes, except for a decrease in distance (33.5 cm) by wild salmon in the presence of hatchery salmon (Table 2). In trout, the distance to nearest neighbor was greatest (31.7 cm) in allopatric populations, less in sympatric populations with wild salmon (26.3 cm), and least in the presence of hatchery-reared salmon (22.5 cm). The mean distance to nearest neighbor for trout (26.8 cm) was typically less than for salmon (36.8 cm) at any time.

Using average number of interactions per individual as a

TABLE 3. Percentage wins by dominant and subordinant fish against other dominant (dom) and subordinant (sub) individuals in sympatric populations, from the Matamek River, 1979.

Interactions by	Percent wins against: Salmon wild dom	Trout dom	Salmon wild sub	Trout sub
A) salmon wild and trout				
	Dominants			
Salmon wild	—	13.7	50.3	35.9
Trout	3.6	—	42.7	53.6
	Subordinants			
Salmon wild	10.4	13.0	26.0	50.6
Trout	6.8	11.0	60.3	21.9

Interactions by	Percent wins against: Salmon wild dom	Salmon hatchery dom	Salmon wild sub	Salmon hatchery sub
B) salmon wild and salmon hatchery				
	Dominants			
Salmon wild	—	12.1	35.0	52.9
Salmon hatchery	10.6	—	39.8	49.7
	Subordinants			
Salmon wild	17.3	13.5	19.2	50.0
Salmon hatchery	32.0	16.5	45.4	6.2

criterion (Table 2), the test populations can be separated into three groupings. The lowest level of interaction (approximately 8 interactions per individual) includes wild salmon alone (8), hatchery-reared salmon alone (6), and both population mixes of wild salmon and trout (8 and 9). The middle grouping (approximately 13 interactions per individual) includes hatchery salmon in sympatry with trout (14) and wild salmon (12) and trout and wild salmon in sympatric populations which contain hatchery-reared salmon (12 and 12). The greatest level of interaction (an average of 30 per individual) was found in allopatric trout populations.

In all sympatric populations, a dominant individual of each species or type was apparent. These individuals were usually observed holding station at the upstream end of the flume sections. The subordinants of both species or types were found at more downstream locations in the flume sections where they overlapped and interacted with each other. Dominant salmon, whether hatchery-reared or wild, were strongly territorial but dominant trout were less so. Dominant wild salmon interacted little with the dominant trout, while the subordinant fish of both species interacted among themselves and with both dominant fish (Table 3*a*). The same trend was observed in sympatric populations of wild and hatchery-reared salmon (Table 3*b*).

The number of successful interspecific and inter "type" interactions was split evenly in sympatric populations of wild salmon and trout (12.6 vs. 13.6) and hatchery-reared salmon with wild salmon (21.9 vs. 20.5); neither participant having an advantage over the other (Table 4). The same was not true in populations of hatchery-reared salmon with trout, where the trout were more successful (20.9 vs. 14.4) than the salmon. Hatchery-reared salmon interacted more with trout or wild salmon than did the latter two with each other (Table 4).

Discussion

Behavioral modifications which occur in juvenile wild Atlantic salmon when hatched and reared under prevailing hatchery conditions are of particular ecological significance when these fish are released into streams. So distinctive are the changes that the fish behave as a different species in their environmental demands and interactions with wild Atlantic salmon and brook trout.

The foremost behavioral difference is the selection of stream stations just off the bottom in continuous current. This is in contrast to the positioning of wild salmon juveniles in contact with the bottom, and the locating of wild brook trout juveniles higher in the water column in either slower flowing or less turbulent water. Hence, the hatchery-reared salmon must contend, more or less, with maximum current velocities requiring sustained swimming effort and high energy demand. As hatchery-reared salmon have a less varied diet than wild juveniles (Sosiak et al. 1979) which is presumably related to a scope of "search images" encountered in the hatchery (Ware 1971), it may be speculated that the lesser repertoire of search images by the hatchery-reared fish may limit, at least initially, the extent and efficiency of feeding by released fish. The lack of natural experience on the fright behavior of hatchery-reared salmonids has been previously noted by Ritter and MacCrimmon (1973).

A further ecological disadvantage of the off-bottom partitioning by hatchery-reared juvenile salmon is a vulnerability to the full force of freshets which, according to Elson (1940), are correlated with the downstream movement and loss of planted Atlantic salmon fry. While the extent of suitable habitat will determine the juvenile carrying capacity of salmonid streams (McCrimmon 1954; Millard and MacCrimmon 1972), the peculiar behavior of hatchery-reared juveniles described here is undoubtedly a factor affecting the limited survival of such fish when released in salmon rivers (Harris 1973).

The considerable differences which our study has revealed in the behavior of hatchery-reared from wild salmon in allopatry, and especially in sympatry with wild salmon and brook trout juveniles, could probably affect their growth and survival potential in streams. Gibson (1973) noted the preference of wild salmon and trout for bottom and off-bottom habitats, respectively, which limits interactions. The intermediate (just off-bottom) stationing of the hatchery-reared juveniles, however, places them in a more competitive position with wild juveniles of both salmon and trout. Higher levels of aggression occurred between hatchery-reared salmon and wild fish of either species than between wild salmon and trout. The level of aggression between wild salmon and trout agrees with Pianka's (1978) statement that overlap in environmental demands, and hence aggression, decreases with taxonomic distance. However, the rates of interaction for hatchery-reared salmon do not follow Pianka's (1978) predictions, as the level of interaction between hatchery-reared and wild salmon (conspecifics) is the same as between hatchery-reared salmon and trout (confamial).

Thus, hatchery-reared salmon released into streams are faced with a level of aggression with trout not experienced by

TABLE 4. The total number of interactions per trial in the mixed tanks, with breakdown by species, and within species to inter–intra-specific interactions (with percentages) from the Matamek stream tank, 1979.

Population type[a]	Behavioral interactions						
	Interspecific		Intraspecific			Subtotal	
	Salmon	Trout	Salmon	Trout	Total	Salmon	Trout
Sw/T							
$\bar{x}$	12.6	13.6	12.4	11.5	50	25.0	25.1
(SD)	(9.7)	(12.9)	(7.4)	(13.9)	(33.9)	(17.0)	(23.2)
n	5	5	5	5	5	5	5
%	48.1	51.9	—	—	—	49.9	50.1
Sh/T							
$\bar{x}$	14.4	20.9	26.1	15.0	76.8	40.5	35.9
(SD)	(9.3)	(9.7)	(20.4)	(20.3)	(17.3)	(23.5)	(24.3)
n	5	5	5	5	5	5	5
%	40.8	59.2	—	—	—	53.0	47.0
Sw/Sh[b]							
	Intertype		Intratype				
	Sw	Sh	Sw	Sh		Sw	Sh
$\bar{x}$	20.5	21.9	9.1	14.4	65.9	29.6	36.3
(SD)	(18.4)	(19.3)	(4.64)	(11.10)	(33.0)	(15.2)	(29.9)
n	4	4	4	4	4	4	4
%	48.3	51.7	—	—	—	44.9	55.1

[a] T, Trout; Sw, Salmon wild; Sh, Salmon hatchery.
[b] Only trials 3–6.

wild salmon, and there is no evidence of an integrated social structure as observed by Newman (1956) for sympatric populations of rainbow (*Salmo gairdneri*) and brook trout. Our findings are in line with the belief of Elson (1975) that newly-planted salmon juveniles were displaced because wild resident juveniles were more aggressive. Interactions of hatchery-reared salmon were even less successful with the brook trout in off-bottom situations to which the latter species was fully adapted, resulting in a displacement of the salmon.

While not statistically significant, it appears that the growth of salmon was better in allopatric rather than sympatric populations in the simulated stream habitats. Attacks by dominant fish on subordinates within both the hatchery-reared and wild salmon populations did not persist and interaction among individuals was less in allopatry. This fact, also found for rainbow trout juveniles by Jenkins (1971), would seem to result in less stress and, hence, a better opportunity for conversion of energy to growth. Miller (1958) postulated that competition of released hatchery-reared cutthroat juveniles (*Salmo clarkii*) with wild fish caused stress (lactic acid build-up) which was a significant cause of mortality. Symons (1969) observed that planted juvenile Atlantic salmon, unlike other salmonids (Chapman 1962; Mason and Chapman 1965), tended to stay where first released in streams. This behavior would be expected to increase the likelihood of sustained contact with wild salmon and trout juveniles and the probability of interactions detrimental to the welfare of the hatchery-reared fish.

Hence, the present findings provide quantitative evidence that the progeny of wild Atlantic salmon reared in hatcheries develop a modified habitat selection and behavior pattern different from wild juveniles. While these ecophenotypic expressions appear disadvantageous to the welfare of the hatchery product when exposed to natural stream conditions, it is equally possible to develop or reenforce advantageous behavioral characteristics by the modification of existing hatchery design and technology. This is an aspect of Atlantic salmon management where more intensive research and refinement is long overdue.

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Release of Methyl Mercury from Sediments: Effects of Mercury Concentration, Low Temperature, and Nutrient Addition

DAVID R. WRIGHT[1]

Department of Microbiology, University of Manitoba, Winnipeg, Man. R3T 2N2

AND R. D. HAMILTON[2]

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6

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A flow-through system using plexiglass "microbasins" was used to study methyl mercury release from unpolluted, mercury polluted, and mercury enriched lake and river sediments. Production of methyl mercury ranged up to 3.3 $\mu g \cdot m^{-2} \cdot d^{-1}$, increasing with increasing mercury content as if following saturation kinetics. It leveled off when mercury content was 15–20 μg Hg/g. An equilibrium between methylating and demethylating mechanisms is suggested. Release at 4°C was 50–70% of that at 20°C, which suggests that in polluted Canadian lakes, production in winter may be half the total for the year. Increased methyl mercury release was observed when tryptic soy broth (TSB) was added to sediments at 0.06 or 0.25 g/dm^3, and very marked increases when TSB was added to the water flow at 35 mg/L, suggesting an effect at the sediment–water interface.

Key words: mercury, methyl mercury, methylation, microbasin, microorganism, sediments, biomethylation

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La mise en liberté de mercure-méthyl de sédiments lacustres et fluviaux non pollués, pollués par le mercure ou enrichis au mercure a été étudiée à l'aide d'un système à débit continu constitué de «microbassins» en plexiglass. La production de mercure-méthyl varie entre 3,3 $\mu g \cdot m^{-2} \cdot d^{-1}$, augmentant en même temps que la teneur en mercure comme si elle suivait une cinétique de saturation. Elle atteint un plateau au moment où la teneur en mercure atteint 15–20 μg Hg/g. Il semble y avoir équilibre entre les mécanismes de méthylation et de déméthylation. La mise en liberté à 4°C est de 50–70% de ce qu'elle est à 20°C, ce qui donne à penser que, dans les lacs canadiens pollués, la production hivernale peut représenter la moitié du total de l'année. On observe une plus grande quantité de mercure-méthyl libéré quand on ajoute aux sédiments un bouillon de soja tryptique (TSB) à 0,06 ou 0,25 g/dm^3 et des augmentations très prononcées quand le TSB est ajouté au débit d'eau à 35 mg/L, ce qui laisse supposer un effet à la surface de contact sédiment–eau.

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MANY lake and river systems contain undesirable levels of mercury (Goldwater 1971; Katz 1972; Fishbein 1974). Almost all of the metal is found in the sediments, and may be of natural occurrence or result from human activities (Bertine and Goldberg 1971; Gavis and Ferguson 1972; Lexmond et al. 1976). Fish and other aquatic biota in such contaminated systems often have elevated levels of mercury (Jensen and Jernelov 1969; Fimreite et al. 1971; Keeney 1972). While mercury in the watercourse is present predominantly in inorganic form, an organo-mercurial neurotoxin (methyl mercuric ion) is the form usually identified as being present in contaminated aquatic organisms (Westöö 1969; Fimreite et al. 1971).

The net production of methyl mercury is generally believed to be biologically controlled (Jensen and Jernelov 1969; Spangler et al. 1973a, b; Billen et al. 1974; Wood 1974) and it is thought that the important site for methyl mercury

[1]Present address: Howard, Mackie, Barristers and Solicitors, 7th Floor, 801 7th Avenue S.W., Calgary, Alta. T2P 2N6.

[2]Requests for reprints should be directed to the Freshwater Institute.

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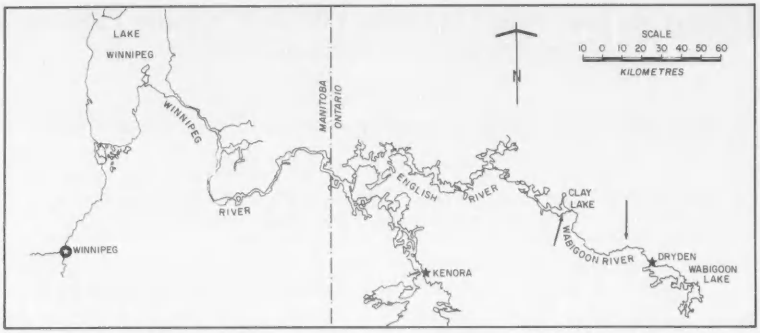

FIG. 1. English–Wabigoon River system. Flow is from Dryden to Lake Winnipeg. Arrows represent the sediment sampling locations.

production is in mercury laden sediments (Jernelov 1972; Jernelov et al. 1975). Although pure culture studies have shown that certain specific microorganisms native to sediments have the potential to methylate inorganic mercury, it has not been conclusively demonstrated that these are in fact the organisms responsible for the observed in situ production. From these investigations it is difficult to predict what effect the alteration of physical and chemical factors in sediment will have in terms of the degree of methyl mercury enrichment in organisms in nature.

To study the kinetics of the overall methylation process, an approach was developed where the effect of physical and chemical factors upon natural mercury contaminated sediments can be observed through changes in the net release of methyl mercury from sediment. Moreover, nonbiological production of methyl mercury is possible (Imura et al. 1971; Bertilsson and Neujahr 1971; Schrauzer et al. 1971) and demethylation processes also occur (Spangler et al. 1973a, b; Billen et al. 1974). Laboratory studies using small-scale systems with water, sediment and fish (Miller et al. 1979) have shown that the chemical characteristics of the sediment largely govern the methyl mercury concentrations in water and fish. The net rate of production of methyl mercury in similar systems has been measured by Bongers and Khattak (1972) and by Langley (1973). More elaborate experiments (Bisogni and Lawrence 1975) have allowed evaluation of reaction kinetics with variations in temperature, COD loading, mercury application, and sulphide concentration.

To investigate further the methylation process we have developed systems in which natural, polluted, or mercury enriched sediments could be held for some months under slowly flowing lake water, and the release of methyl mercury measured by analysis of the effluent. By this means we have been able to demonstrate something of the phases of the process and of its kinetics, and of effects of low temperatures and of the addition of bacterial nutrient to the system.

The work in the report has been described in thesis form (Wright 1978).

Materials and Methods

SEDIMENTS USED

Mercury contaminated sediments were obtained during May to October (1977) from the mercury contaminated Wabigoon River and Clay Lake (50°04′N, 93°30′W) in Northwestern Ontario (Fig. 1). They are fine clays with varying proportions of wood debris from a pulp-mill operation (Armstrong and Hamilton 1973; Parks 1976). Most sediment samples were collected with a modified Ekman dredge (Burton and Flannagan 1973). Material from the top 6–8 cm of the lake and river beds, where most of the mercury is located, was collected. Samples were transported to the laboratory in polyethylene-lined 2-gal pails. The Wabigoon River sediment samples contained 4 μg Hg/g (dry weight), those from Clay Lake 3 μg/g. Sediments with a low mercury content (approx. 100 ng Hg/g) were obtained from Rawson Lake, L 239 in the Experimental Lakes Area (ELA) at 49°40′N, 93°44′W. The analyses are for total mercury determined by the AAS automated procedure of Armstrong and Uthe (1971) after the aqua regia extraction method of the Dow Chemical Company (Anon 1970).

EXPERIMENTAL DESIGN

Rectangular plexiglass boxes ("microbasins"), internally 100 cm long, 20 cm deep, and 10 cm wide, were utilized in the study (Fig. 2). One end of the microbasin was removable for the introduction of sediment. In experiments requiring higher levels of mercury, the sediment was enriched by adding $HgCl_2$ solution (0.05 mg Hg/mL) during filling. When the microbasin was filled to 80% capacity, the basin end was screwed on and sealed with RTV 108 silicone rubber adhesive (General Electric, Waterford, NY). The microbasin was shaken by hand for 5 min and then allowed to settle for 1 d. Sampling for analysis was carried out through small holes in the top of the basin.

After the settling period, water was pumped over the surface of the sediment in the basin at the rate of 1 L/24 h (approx. 0.7 $mL \cdot min^{-1}$) resulting in a residence time within the microbasin of about 60 h. Basins were set up in groups of up to 10 microbasins (Fig. 3) and water from a reservoir was introduced through a glass manifold (1 entrance, 12 exits) by a Manostat cassette pump (Manostat, New York, NY).

The sampling holes in the top of one microbasin, which were sealed with masking tape during normal basin operation, were also utilized for an aeration experiment. Clean air was

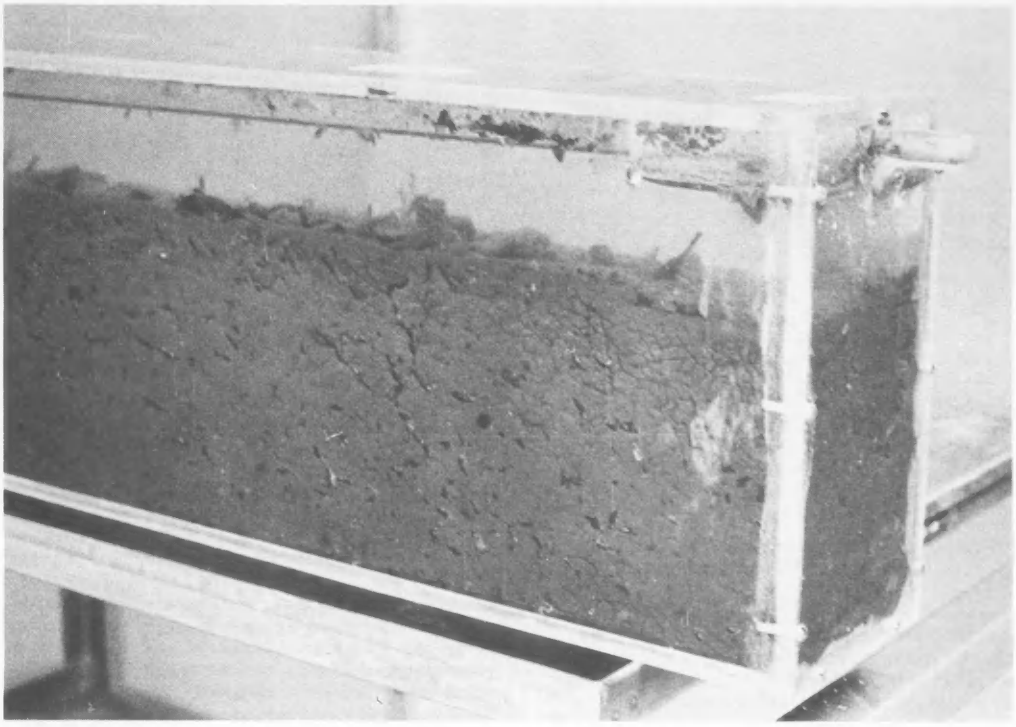

FIG. 2. Microbasin containing Wabigoon River sediment. The removable end of the basin, used during the basin set-up process, is shown in the figure. During basin operation L239 water flowed over the sediments and was released from the basin by way of the outflow port (upper right). Also shown in the figure is gas trapped at the top of the basin, after release from the sediments. The masking tape on the top of the basin covers holes through which sampling of sediments was carried out. The overall basin dimensions were 100 × 10 × 20 cm.

driven with a Cole-Parmer peristaltic pump (Cole-Parmer Instrument Co., Chicago, IL) through one hole, over the surface of the water layer in the basin, and out at the other end of the microbasin. The flow rate was approximately 50 cm^3/min.

The water used in all studies was from Rawson Lake (Armstrong and Schindler 1971).

Effluent from each microbasin was collected so that the water flow through individual basins could be monitored daily. Volumetric flasks (1 L) were utilized to collect effluent over 24 h for analysis as to the net release of methyl mercury from the sediment in the microbasin to the water flowing through the basin. The effluent collected was divided into either two 500-mL or four 250-mL aliquots which were analyzed as to methyl mercury content. Therefore, each point obtained represented at least two, and often four, analyses from which similar results were obtained. The variation in data obtained from these independent analyses was within 5–15%. The analyses were converted to arrive at a determination of the concentration of methyl mercury being released from each microbasin over a 24-h period. The curves illustrated in the Figures were fitted to the points by eye.

Microbasin effluent was analyzed on a weekly basis, except for long-term basin experiments in which case samples were analyzed on approximately a bimonthly basis. The loss of methyl mercury from the volumetric flasks over the 24-h collection period was found to be 10%.

METHYL MERCURY ANALYSIS

Methyl mercury was extracted by the method of Uthe et al. (1972). Analysis was by GLC with electron capture detector. The extraction efficiency was 67% and results were corrected for this.

All glassware used in the analysis for methyl mercury was washed with H_2SO_4 (conc.), $Na_2S_2O_3$ (3 mol/L), and rinsed thoroughly with distilled water.

Toluene and benzene used were pesticide grade from Caledon Laboratories Ltd. (Georgetown, Ont.). Standardization was with methyl mercuric chloride (95%) from Alfa Inorganics (Danvers, MA), and all other chemicals were Baker "analyzed." Low temperature experiments were done with microbasins in a waterbath maintained at 4±1°C.

Two separate series of nutrient enrichment experiments were done with Tryptic Soy Broth (TSB, Difco). In the first, TSB was added directly to the sediments when setting up, to

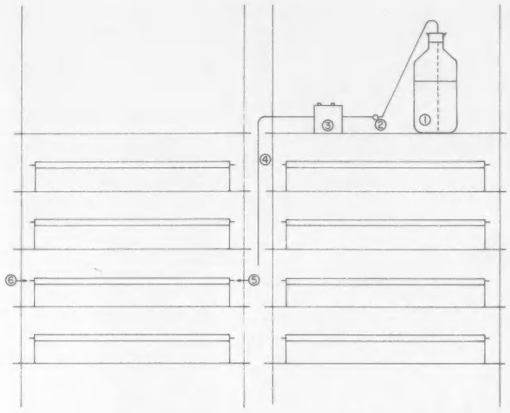

FIG. 3. Schematic diagram of the microbasin flow-through system: (1) L239 water reservoir; (2) manifold; (3) cassette pump; (4) water line to a basin; (5) microbasin inflow; (6) microbasin outflow.

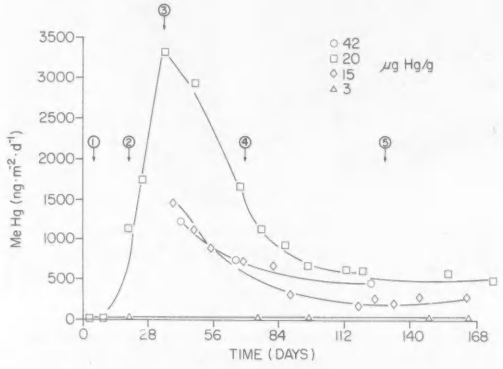

FIG. 4. Net release of methyl mercury from Clay Lake sediment with added mercury as a function of time showing (1) lag; (2) exponential; (3) maximum; (4) decrease; and (5) level-off phases.

give 1 or 4 g TSB per microbasin of approx. 16 L sediment. In the second series the TSB addition was made only to the lake water flowing through, being approximately 35 mg TSB/L.

Results

Effect of Mercury Concentration on Net Methyl Mercury Production

The release of methyl mercury as a function of time from Clay Lake and Wabigoon River mercury-laden sediments (Fig. 4 and 5) characteristically demonstrated a lag during the first week, an increase to a maximum at about 4 wk, followed by a decrease to a steady lower level related to mercury concentration. However, the maximum rate of methyl mercury release was difficult to pinpoint in some microbasin experiments owing to the very significant change in methyl mercury release over a short period of time. As well, the turbidity of effluent from microbasins, particularly with Clay Lake sediments, during 2–3 wk following the setting up of a microbasin resulted in interference with methyl mercury analysis. Therefore, the emphasis in later microbasin experiments was an analysis of methyl mercury release during the level-off phase when release of methyl mercury over the long term from sediment at a particular mercury concentration was relatively constant. Methylation increased more steeply than mercury concentration in sediment, up to approximately 20 μg Hg/g, after which it decreased slightly.

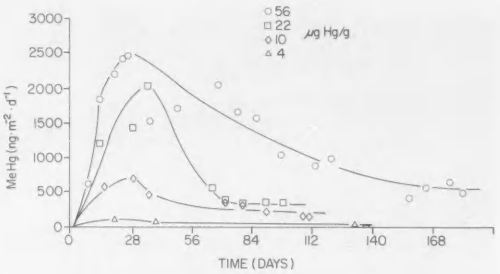

FIG. 5. Net release of methyl mercury from Wabigoon River sediment with added mercury as a function of time.

TABLE 1. Total mercury in effluent from microbasins containing Wabigoon River sediment.

μg Hg/g sediment	ng Hg/mL effluent
56 (nonaerated)	0.413
23 "	0.458
10 "	0.238
4 "	0.317
4 (aerated)	1.144

Effect of Aeration

Above the water in a microbasin there exists a space where gas evolved from sediment in the basin accumulates and is effectively trapped (Fig. 2). A microbasin appears as an almost anaerobic system with a small supply of oxygen from that dissolved in the water flowing through.

An aerated Wabigoon River microbasin (4 μg Hg/g) was found during the level-off phase to release approximately 60 $ng \cdot m^{-2} \cdot d^{-1}$ of methyl mercury. Clay Lake and Wabigoon River microbasins at similar sediment mercury concentrations released methyl mercury at approximately the same rate (Fig. 4 and 5). The aerated basin effluent was, however, much more turbid and showed a higher release of total mercury (Table 1). This is possibly due to the observed higher activity of benthic animals (primarily oligochaetes) in it. Although these benthic invertebrates were present in all basins, their survival and activity was greater in the aerated microbasin. However, their activity seemed to have no effect on the level of methyl mercury released.

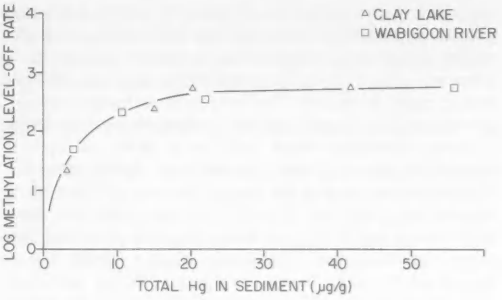

FIG. 6. Maximum and level-off net methyl mercury release/logarithmic scale, of Clay Lake and Wabigoon River sediments against total mercury concentrations.

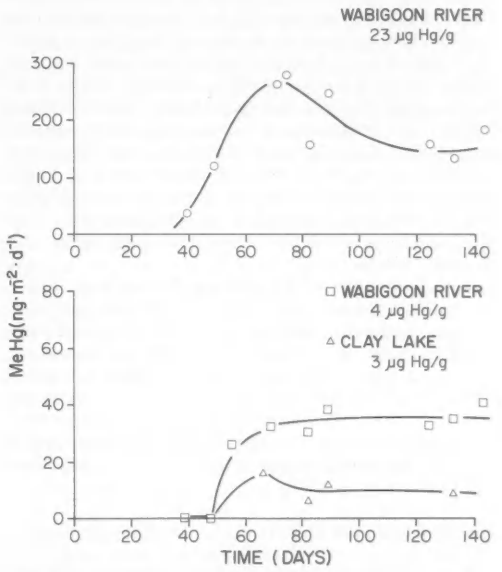

FIG. 7. Net release of methyl mercury at 4°C as a function of time from Wabigoon River and Clay Lake sediments.

TABLE 2. Percent net methyl mercury release, in microbasin effluent, at 4°C relative to 20°C (using level-off values from Fig. 7).

	μg Hg/g in sediment	%
Clay Lake	3	63
Wabigoon River	4	70
Wabigoon River	23	50

OVERALL RELEASE OF METHYL MERCURY IN THE ENGLISH–WABIGOON RIVER SYSTEM

The sediment in the Wabigoon River, containing much wood chip and fiber, differs significantly from the smooth clay sediments of Clay Lake. Regardless of sediment origin, however, the net methyl mercury release observed from a given total mercury concentration was characteristic of the total mercury concentrations in sediment (Fig. 6). A rapid increase in net methyl mercury release in the range of up to 15–20 μg Hg/g sediment (dry wt) was observed whereas no further rise in methyl mercury release was found at concentrations greater than 20 μg/g.

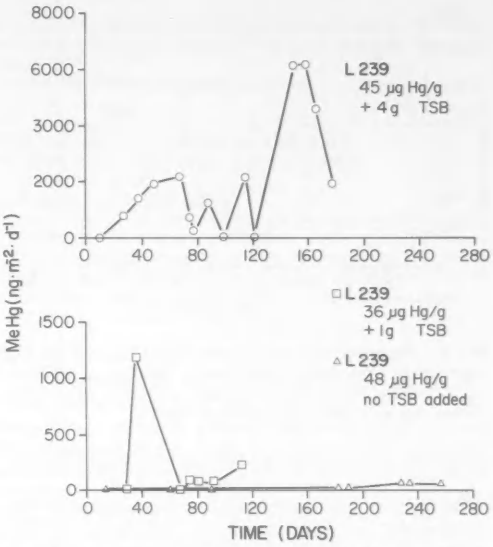

FIG. 8. Net release of methyl mercury from L239 nutrient (TSB) and/or mercury enriched sediments as a function of time.

EFFECT OF 4°C INCUBATION UPON NET METHYL MERCURY RELEASE

The net production of methyl mercury in 4°C incubated microbasins is shown in Fig. 7 and Table 2. The net methyl mercury levels observed at 4°C (Fig. 7) are approximately 50–70% of those obtained from similar sediments at 20°C (Table 2).

EFFECT OF DIRECT TSB ADDITION TO RAWSON LAKE SEDIMENTS

Sediments were enriched with mercury so that methyl mercury release from newly contaminated sediments could be measured. These experiments were carried out at 20°C. As shown in Fig. 8, net methyl mercury release from Rawson Lake sediment enriched to 48 μg Hg/g (dry wt), over an 8-mo period, was extremely low (less than 40 $ng \cdot m^{-2} \cdot d^{-1}$). However, when Rawson Lake sediments were enriched with TSB as well as mercury during the basin set-up process, net methyl mercury release was greatly enchanced (Fig. 8). Although net methyl mercury release fluctuated considerably in these experiments, the release from the enriched (4 g TSB) basin was approximately 100× that of sediments which had not been enriched.

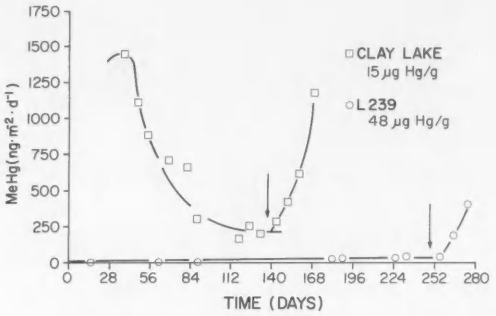

FIG. 9. Net release of methyl mercury from Clay Lake and L239 sediments as a function of time, showing the effect of addition of (approximately) 35 mg TSB/microbasins per day to inflow water. Arrows indicate when nutrient addition began.

EFFECT OF TSB ADDITION TO MICROBASIN INFLOW WATER

The Rawson Lake water passing over the surface of mercury contaminated Rawson Lake sediments was enriched with TSB (approx. 35 mg TSB/d). Prior to the nutrient addition the Rawson Lake basin had released only a minimal amount of methyl mercury but as shown in Fig. 9, the addition of nutrient resulted in an immediate increase in methyl mercury production. Clay Lake sediments, from which methyl mercury release had declined greatly from its maximum and appeared to be leveling off at a low value, showed a great increase when exposed to water containing TSB.

Discussion

MICROBASIN DYNAMICS

The lag phase observed during the week after the setting up of a basin, which is particularly discernible in Fig. 7 and 8, can probably be attributed to the effects of handling and mixing of the sediment during the collection, transport, and microbasin set-up process. The lag would be particularly pronounced where microbiological communities responsible for methyl mercury production are stratified with respect to chemical and physical features in sediment, such as oxidation-reduction potential, for example. During the lag period in methyl mercury release a small amount of a compound tentatively identified (from its elution time in the gas-chromatograph) as ethyl mercury was detected. It was transitory, disappearing as soon as methyl mercury production began, and it appeared as though a succession of microorganisms was occurring or that microorganisms were adjusting their metabolism to changing conditions.

The presence of demethylating microorganisms in methyl mercury-producing sediments has been clearly documented (Billen et al. 1974; Spangler et al. 1973a, b). Spangler et al. (1973b) showed that after an initial increase in methyl mercury levels over a 1.5-mo period, the level of methyl mercury in batch flask-sediment cultures dropped drastically. This decrease corresponded directly to an increase in elemental mercury released and the authors concluded that demethylating organisms were responsible. Billen et al. (1974) conducted experiments dealing with an observed methyl mercury mineralizing activity and concluded that in mercury polluted environments an equilibrium between methylation and mineralization might be reached. The decrease in net methyl mercury production (Fig. 4 and 5) and the resulting steady-state levels observed thereafter might well be a result of such a methylating-demethylating (mineralizing) equilibrium. We have shown here that in the range of up to 15–20 μg Hg/g there is an increase in net methyl mercury production more rapid than a simple proportionality between production and mercury concentration in sediment. Jernelov (1969), Jensen and Jernelov (1969), Jacobs and Keeney (1974), and Olson and Cooper (1974, 1976) have similarly shown that an increased mercury concentration in sediment results in a rise in methyl mercury production.

The mercury concentration range examined in our study is within that observed to occur in nature. Armstrong and Hamilton (1973) found that the mean mercury concentration in Clay Lake sediments examined was 3.1 μg Hg/g, with a range from 0.1 to 7.8 μg Hg/g. Our results show that sediments with high concentrations of mercury in Clay Lake (6–8 μg Hg/g) may be "hot spots" for the release of methyl mercury. We estimate that 9% of the total sediment surface area of Clay Lake (which is at approx. 7 μg Hg/g) may contribute about 40% of the total net production of methyl mercury in the entire lake on a per unit time basis. This effect may be even more important in the Wabigoon River where mercury content of sediment varies greatly from one location to another (Parks 1976).

It has been estimated that there are about 2000 kg of mercury in Clay Lake sediments (Armstrong and Hamilton 1973). If the rates of net methyl mercury production in lakes and rivers are at all similar to those observed in our experiments, the fraction of total mercury released by sediments as methyl mercury on a yearly basis, though very small (probably less than 0.1%), may yet amount to some kilograms, quite sufficient to contaminate the fish population to unsafe levels. Other investigators have made a similar estimate of this fraction (Jernelov et al. 1975).

METHYLATION OF MERCURY AT 4°C

It has been shown that methyl mercury production increases rapidly with a rise in temperature (Bishop and Kirsch 1972; Fagerstrom and Jernelov 1972; Shin and Krenkel 1976). However, when considering methylation in lakes in Canada where for a large portion of the year water temperature is 4°C, information concerning methyl mercury production at low temperatures is essential. In our experiments net methyl mercury release at 4°C is 50–70% of that at 20°C. Assuming a temperature in Clay Lake of 4°C for 8 mo of the year and 20°C for 4 mo for example, then over half of the total yearly methyl mercury burden upon aquatic organisms may be from low temperature methylation.

That methyl mercury production at low temperatures is so high should not be surprising as most investigators believe that microorganisms use the methylation process to detoxify their environment of mercury (Landner 1971; Wood 1974; Wood et al. 1978). At low temperatures microorganisms may have to utilize a greater percentage of their available energy

for methylation to protect themselves from mercury's toxicity. Methylation may not necessarily be linear with respect to temperature. Additional low temperature methylation data supports this conclusion (Shin and Krenkel 1976).

Methylation of Mercury with Nutrient Addition

It is thought that nutrient availability is an important factor in microbiological methylation (Fagerstrom and Jernelov 1972). We found that over an extended period of time, Rawson Lake mercury-contaminated sediments released very little methyl mercury but that the direct addition of 1 or 4 g TSB during the basin set-up process (Fig. 8) resulted in large methyl mercury releases after (approximately) 30 and 12 d of basin operation, respectively. We also found that the addition of a much smaller amount of nutrient (35 mg TSB/d) to the inflow water of the Rawson Lake microbasin which had shown a very low net methyl mercury production for over 240 d, caused a rapid increase in methyl mercury release (Fig. 9).

Other investigators as well have shown that methyl mercury production rises as nutrient levels increase (Jensen and Jernelov 1969; Jernelov 1972; Bishop and Kirsch 1972). However, our results indicate that the overall concentration of nutrients in mercury methylating sediments is not so important as is the amount of nutrient available for microbial activity near the sediment–water interface. We believe methyl mercury released to the water column to be that produced in the top layers of the sediments. Although the methylation process might be active to great depths within sediments, it may well be that much of the methyl mercury produced more deeply in sediments is destroyed through demethylating activities prior to its release from the sediments. This is probably why the covering of methyl mercury producing sediments with clean sediments can be an effective means of reducing sediment methyl mercury releases (Jernelov 1970).

Relationship Between Nutrient Additions to Natural Systems and Methyl Mercury Levels in Aquatic Organisms

Approximately 9 000–11 000 kg of inorganic mercury were released to the English–Wabigoon River system during 1962–70 from a pulp and paper mill-chlor-alkali complex in the town of Dryden (Armstrong and Hamilton 1973). The mercury releases have ended but the river system is still subjected to large discharges of organic matter from the pulp and paper mill. For example, Parks (1976) notes that the average 1975 BOD_5 800 m above the mill was 0.88 mg/L whereas it was 28 mg/L 1100 m below the mill.

The microbasin nutrient addition experiments raise the question of what will be the result when a biologically oxidizable substrate is added to a mercury polluted river or stream in nature. As can be seen from Table 3, the amount of organic carbon (added as TSB) in the microbasin experiments (Fig. 9) is at about the same level as that appearing in the Wabigoon River just downstream from the pulp and paper mill outfall. These experiments clearly show that the addition of nutrient at this level resulted in immediate increases in the release of methyl mercury from Clay Lake and Rawson Lake mercury contaminated sediments.

Table 3. Comparison of total dissolved organic carbon (DOC) levels used in microbasin experiments with that found in the Wabigoon River.

	mg DOC/L
Wabigoon Lake (2 km upstream from Dryden)	5
Wabigoon River (4 km downstream from Dryden)	18
L239 reservoir water[a]	6
L239 water + TSB addition[b]	24

[a]Courtesy of ELA chemistry laboratory.

[b]This is a maximum amount of TSB (assumed to be 50% DOC) added to nonsterile L239 water in the reservoir. The TSB — L239 reservoir was cleaned, and fresh TSB — L239 water was made up every 48 h.

These experiments with addition of nutrient support the assumption which we have made throughout this work, that the process is primarily a result of microbiological activity. Direct evidence of this could have been provided by first sterilizing sediment and determining if abiotic production of methyl mercury occurs under sterile conditions. However, the difficulty of keeping sterile such a large amount of sediment and water would be enormous, and would produce such physical and chemical changes in the material that interpretation of the results would be most difficult.

We believe that these laboratory results are indicative of what can be expected to be observed in a natural system. The effect of temperature upon the methylation process is small when considering the entire river–lake system. However, elevated concentrations of mercury in sediments and increased inputs of organic matter to the Wabigoon River probably result in an elevated methyl mercury burden upon aquatic organisms within the river system. Therefore, we suggest that a reduced discharge of organic materials into the river system will decrease the level of methyl mercury in downstream fish.

The Microbasin System as a Tool

Most of the previous work on methyl mercury production in sediment involved the analysis of mercury contaminated sediment for total methyl mercury content. Wood (1974) suggests that measuring the concentration of methyl mercury in sediment is meaningless, since the measured concentration may not be indicative of the rate of synthesis if methyl mercury is at a near steady-state level in sediment. In our study with a flow-through system, we have looked only at the net release of methyl mercury from sediment, which may be expected to be available for uptake by aquatic organisms.

There are two ways in which information from microbasins can be used. The first is to try to relate the actual numbers obtained directly to the methylation process in nature. This may be the least useful way in which basin results can be utilized since microbasins are artificial systems. Of greater importance than the extrapolation of numbers to nature is using the microbasin system to demonstrate the basic kinetics of the overall methylation process, and to measure the effects of changes in the system.

Microbasins appear to be useful for testing proposed amelioration methods, such as covering up sediments, ploughing them to depth, or treating them chemically. With the advan-

tage of using a flow-through system and chemical analysis, they are also easy to maintain and are inexpensive.

Acknowledgments

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Stock Reduction Analysis, Another Solution to the Catch Equations

DANIEL K. KIMURA AND JACK V. TAGART

Washington Department of Fisheries, Olympia, WA 98504, USA

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In fishery stock assessments, catch equations provide the critical link between stock size, natural mortality rate, fishing rate, and catch size. Catch equations are most powerful when age data are available, allowing cohorts to be followed through time using Virtual Population and Cohort Analysis. In this paper we propose a simple new method of linking catch equations when age data are not available. Assuming catches are given in biomass, catch equations are written for each year with a constant recruitment (R), based on a single parameter, added to the total biomass at the beginning of each year. In addition to the catch equations, a final equation is added describing the change in biomass caused by the years of fishing. If n years of catch data are available, $n+1$ equations can be written. By conditioning on instantaneous natural mortality rate (M), initial stock size (B_1) and the decline in stock size (P) (note $P = B_{n+1}/B_1$), the $n+1$ simultaneous nonlinear equations can be solved iteratively for instantaneous fishing mortality rates ($F_1, \ldots, F_n$) and recruitment (R). When properly plotted, the solution set to this system of equations was found to be a helpful tool to aid in the evaluation of stock condition. In particular, the plots provide a method for incorporating ancillary information from diverse sources such as hydroacoustic surveys, analysis of catch per unit effort data, and Virtual Population Analysis. This new method of stock assessment, which we call Stock Reduction Analysis, is applied to Pacific ocean perch (*Sebastes alutus*), Pacific herring (*Clupea harengus pallasi*), and Pacific hake (*Merluccius productus*) stocks being actively managed by the State of Washington.

Key words: Stock Reduction Analysis, stock assessment, catch equations, computer modeling

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Dans l'évaluation des stocks pêchés, les équations de capture sont un lien critique entre l'importance du stock, le taux de mortalité naturelle, le taux de pêche et le volume des prises. Ces équations sont surtout utiles quand on dispose de données sur les âges, ce qui permet de suivre les cohortes dans le temps par analyse de population virtuelle et de cohortes. Nous proposons dans l'article qui suit une méthode nouvelle simple pour faire le lien entre équations de capture en l'absence de données sur les âges. Dans l'hypothèse que les prises sont données en biomasse, les équations de capture sont notées chaque année avec recrutement constant (R), reposant sur un seul paramètre et ajouté à la biomasse totale au début de chaque année. À ces équations on ajoute une équation finale décrivant les changements que les années de pêche ont imposés à la biomasse. Si l'on dispose de données sur les prises pour n années, on peut donc poser $n+1$ équations. En supposant un taux de mortalité naturelle instantané (M), un effectif initial de stock (B_1) et un déclin d'effectif de stock (P) (à noter que $P = B_{n+1}/B_1$), on peut résoudre par itération les $n+1$ équations non linéaires simultanées pour des taux de mortalité par pêche instantanés ($F_1, \ldots, F_n$) et de recrutement (R). Lorsque proprement portée sur graphique, la solution de ce système d'équations est utile dans l'évaluation de la condition d'un stock. En particulier, les courbes permettent d'incorporer une information auxiliaire provenant de diverses sources, telles que relevés hydro-acoustiques, analyse de prises par unité d'effort et analyse de population virtuelle. On applique cette nouvelle méthode d'évaluation des stocks, que nous appelons analyse de réduction de stocks, à ceux du sébaste

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à longue mâchoire (*Sebestes alutus*), du hareng du Pacifique (*Clupea harengus pallasi*) et du merlu du Pacifique (*Merluccius productus*), stocks gérés activement par l'État de Washington.

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FOR an exploited population of fish the most fundamental statistic is usually catch size, and the most fundamental tool of analysis a catch equation. In a science where little is known with a great deal of accuracy, a great effort is typically made to gather catch statistics that are reasonably correct. During the past three decades, many quantitative methods have been developed to more fully use this data.

Methods that are now widely used and generally accepted include Gulland's Virtual Population Analysis (see Pope 1972), and Pella and Tomlinson's (1969) Generalized Production Model. In addition, trawl and hydroacoustic surveys have been developed into practical tools for directly estimating the biomass of some species.

Despite these advances, progress in fishery stock assessment appears to be limited by the assumptions and data required. Even when sufficient age data are available to perform Virtual Population Analysis, and sufficient effort data are available to perform a Production Model Analysis, the results from these analyses often differ significantly from each other, and from available survey estimates. Because every stock assessment method has notable weaknesses, it is usually unclear where the truth lies. To help offset this situation, we offer a new method of analysis that we call Stock Reduction Analysis (SRA).

The principal advantage of SRA is that it is a simple method that does not require age data, yet it is flexible and has the ability to incorporate different sources of information and examine them for consistency. Essentially, for n years of catch data and an estimate of instantaneous natural mortality (M), SRA allows a plot of B_1, P, and R (where B_1 is initial population biomass, P is the change in biomass due to catches, and R is recruitment biomass) that is consistent with the catch history (i.e. consistent with the exponential form of the catch equations), and expected levels of recruitment. Then, if independent estimates of any of these factors are available (from say, modeling, hydroacoustic surveys, analysis of catch per unit effort, etc.), they can be used to provide new estimates, or can be examined in relation to other factors for consistency.

We have found that once the SRA plot is understood, the visual nature of the method allows a real "feeling" for stock condition, and how stock condition relates to ancillary sources of information. Also, we found SRA particularly useful for fisheries which have developed rapidly, and for which time series of data are extremely short while catches are large. This means an assessment can be made before stocks have been depleted.

Stock Reduction Analysis Model

Let C_i be the catch in year i;
B_i the biomass at the beginning of year i (including recruitment);
F_i the instantaneous fishing mortality rate in year i;
M the instantaneous natural mortality rate;
R the annual recruitment biomass (including new fish and growth);
and P the ratio of final biomass to initial biomass.
Consider the sequence of $i = 1, \ldots, n$ catch equations:

$$(1)\quad C_i = B_i F_i(1 - \exp(-F_i - M))/(F_i + M).$$

Note that B_1 contains the recruitment expected in year 1, and in general,

$$(2)\quad B_i = B_{i-1}\exp(-F_{i-1} - M) + R \text{ for } i > 1.$$

To this set of n equations, add the equation

$$(3)\quad P = B_{n+1}/B_1$$

which describes the decline in population biomass caused by the n years of catches.

We now have $n+1$ simultaneous nonlinear equations (Equations 1 and 3) in $n+4$ unknowns: $M, B_1, P, R, F_1, \ldots, F_n$. Hence, there is no unique solution to this equation set. From a mathematical point of view, any $n+4$-tuple which satisfies the $n+1$ simultaneous nonlinear equations is consistent with those equations. Our strategy will be to solve the equations by first conditioning on M, B_1, and P, and then solve for $R, F_1, \ldots, F_n$. We found the plot of B_1 versus R, for a given value of P, to be particularly useful. The acceptable solution set on this SRA plot must then be reduced by the application of other sources of information.

The application of additional information to this plot has been found to be an effective method of evaluating stock condition. Assuming that B_1 represents virgin biomass, or that catches have been small in years prior to year 1, recruitment would have to be $R = B_1(1 - \exp(-M))$ for the population to have maintained itself. To see this, note that if there were no fishing (i.e. all F_i's were zero) in equation (2), then

$$B_{i+1} = B_1 \exp(-iM) + R(1 - \exp(-iM))/(1 - \exp(-M)).$$

Thus for given values of R and M,

$$R = B_{i+1}(1 - \exp(-M))$$

after sufficient years have passed. The line $R = B_1(1 - \exp(-M))$ we call the expected recruitment line; and on the plots, only combinations of B_1 and P which intersect this line are consistent with the replacement concept. This idea will become clear in the applications given later.

In addition to the expected recruitment line, other sources of information such as survey results, changes in catch per unit effort, results from Virtual Population Analysis, etc., can be used to reduce the acceptable solution set. This will be illustrated by the applications given later.

Once an acceptable solution to the catch equations is determined through SRA, estimates of $F_1, \ldots, F_n$ are available to calculate the usual statistics. For example, exploitation rate can be estimated by

$$\hat{U}_i = \hat{F}_i(1 - \exp(-\hat{F}_i - \hat{M}))/(\hat{F}_i + \hat{M})$$

for all i; and a sequence of biomass estimates is given by

$$\hat{B}_i = \hat{B}_{i-1}\exp(-\hat{F}_{i-1} - \hat{M}) + \hat{R} \qquad i > 1,$$

where $\hat{B}_1$ is the estimate of initial biomass.

Solving the SRA Equations

A few years ago, the solution to the system of $n+1$ simultaneous nonlinear equations required by SRA would have been a difficult, time consuming task. Thanks to modern computer software, this task has been made much easier. If a researcher has access to a high quality mathematical software library such as the International Mathematical and Statistical Libraries (IMSL Inc. 1979), it is easy to write a short Fortran computer program which calls an appropriate subroutine to do the difficult computations.

We have written a small interactive Fortran program that uses the subroutine ZSYSTM (IMSL, Inc. 1979) to solve the SRA equations. ZSYSTM was designed for finding iterative solutions to general systems of m simultaneous nonlinear equations in m unknowns. Because the calculations are complex, the choice of computer software may be critical. The program we have written is available upon request, but can be used only on computers having IMSL.

Our SRA program solves equations (1) and (3) by conditioning on M, B_1, and P (fixing these values), then iteratively finding solutions for $R, F_1, \ldots, F_n$. Generally M is assumed to be a known constant, but the analysis can be repeated for differing values of M. The program was made interactive because convergence to a solution $R, F_1, \ldots, F_n$ was sometimes sensitive to initial values provided to ZSYSTM. We used $F_1^\circ = \ldots = F_n^\circ = 0$ as an initial value for F_i's, and searched for an appropriate initial value for R. Usually $R^\circ = B_1(1 - \exp(-M))$ was tried initially, and after a solution was successfully found, the appropriate neighborhood for R° became clear.

SRA plots (examples in Fig. 1–3) are made by connecting the B_1 versus R relationship for a given P. Although this relationship appears to be linear, the reason for this is unclear. It should be emphasized that the $n+4$-tuple M, B_1, P, R, $F_1, \ldots, F_n$ together form a solution to the SRA equations (1) and (3), but that this solution is not unique.

Generally the $n+1$ simultaneous nonlinear equations solved for SRA, and the equation solver ZSYSTM, appear to be stable. Five catch records have been analyzed using our SRA program, three of which are presented in this paper. In no case was there difficulty in finding a reasonable solution set. One catch record was 22 yr long, thus the SRA equation set consisted of 23 equations.

Applications

The method of SRA described in the preceding sections was applied to three stocks of fish being actively managed by the Washington Department of Fisheries: Pacific ocean perch (*Sebastes alutus*), Pacific herring (*Clupea harengus palasi*), and Pacific hake (*Merluccius productus*). Also, these species make interesting examples because they represent a range of natural mortality rates. The natural mortality rate for Pacific ocean perch has been estimated to be $M = 0.15$ (Gunderson 1977); natural mortality for Pacific herring is believed to be approximately $M = 0.40$ (Pacific Council 1981); and the natural mortality rate for Pacific hake is believed to be approximately $M = 0.65$ (Ketchen 1980; Kimura and Millikan 1977). These estimates of M were assumed in the following analyses.

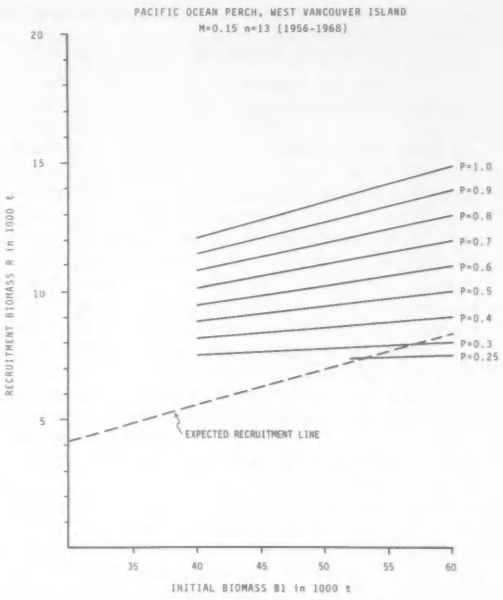

FIG. 1. Stock Reduction Analysis plot for Pacific ocean perch, using data from Table 1.

Tables 1–3 give the area of catch and catch data used for SRA. We assume that catches from these areas are from unit stocks. However, for stocks where immigration and emigration are occurring, analysis based on SRA might still be valid. This is because the net effect of immigration and emigration may only affect apparent recruitment.

PACIFIC OCEAN PERCH, WEST VANCOUVER ISLAND, 1956–69

Figure 1 shows the SRA plot for Pacific ocean perch resulting from analyzing the data in Table 1. The numbers we discuss were read from the plot and are only approximate.

Assuming $M = 0.15$, and B_1 at the beginning of 1956 was less than 60 000 t (as is generally believed), then intersection of the expected recruitment line, with the lines of varying P show stock decline had to be at least 65% from 1956 to 1969 (i.e. $B_{14} = 0.35B_1$). A detailed analysis of CPUE data (Kimura 1981) indicated that by the beginning of 1969, stock size had decreased to $0.25B_1$ (again, B_1 was the biomass at the

TABLE 1. Catch data for Pacific ocean perch in the West Vancouver Island region (Gunderson et al. 1977).

Year	Catch (t)
1956	1 084
1957	1 154
1958	675
1959	968
1960	1 575
1961	2 485
1962	3 857
1963	3 867
1964	2 499
1965	3 546
1966	16 358
1967	13 483
1968	10 417

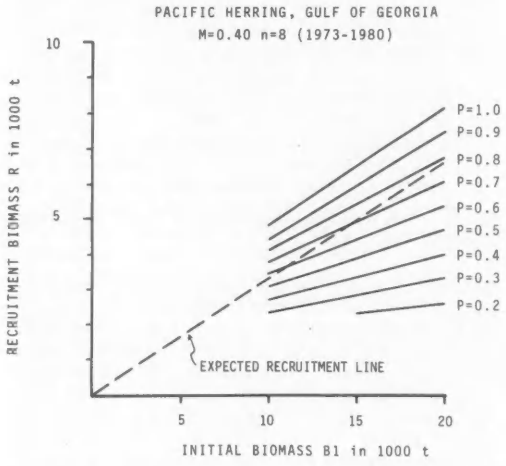

FIG. 2. Stock Reduction Analysis plot for Pacific herring, using data from Table 2.

TABLE 2. Catch data for Pacific herring in the Gulf of Georgia (Pacific Council 1981).

Year	Catch (t)
1973	1 831
1974	3 976
1975	3 570
1976	1 980
1977	2 089
1978	1 934
1979	1 737
1980	1 435

beginning of 1956). If this is correct, the intersection of the SRA plot ($P = 0.25$) with the expected recruitment line indicates that $B_1 = 53\,000$ t at the beginning of 1956, and declined to $B_{14} = 13\,250$ t by the beginning of 1969. Gunderson (1979) estimated 1969 biomass using cohort analysis. His

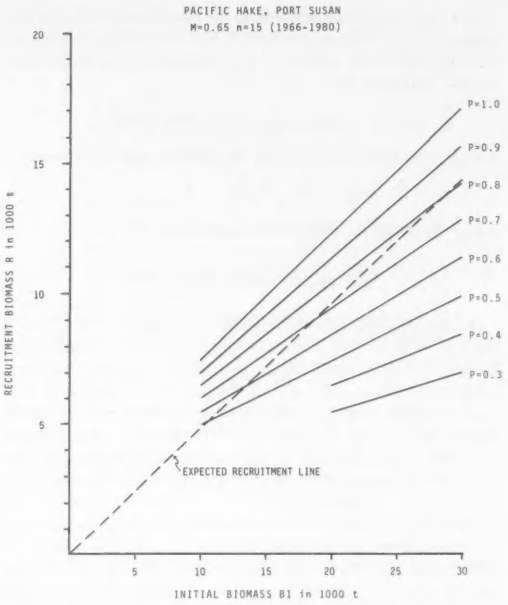

FIG. 3. Stock Reduction Analysis plot for Pacific hake, using data from Table 3.

estimate of 16 581 t is similar to our own.

The SRA program was run using $M = 0.15$, $B_1 = 53\,000$ t, and $P = 0.25$. This run indicated recruitment to be $R = 7{,}397$ t, with 1956 to 1968 F values of 0.022, 0.024, 0.014, 0.021, 0.034, 0.056, 0.092, 0.098, 0.066, 0.097, 0.580, 0.779, and 0.967, respectively.

These F values can be used to estimate annual exploitation rates and biomass, as previously discussed.

PACIFIC HERRING, GULF OF GEORGIA, 1973–81

Figure 2 shows the SRA plot for Pacific herring resulting from analyzing the data in Table 2. Hydroacoustic and spawning ground surveys indicate B_1 at the beginning of 1973 to be approximately 15 000 t (Pacific Council 1981). If $B_1 = 15\,000$ t, expected recruitment intersects the line $P = 0.70$ at a point indicating a 30% stock decline from 1973 to 1981, and an estimated biomass of $B_9 = 0.70 \times 15\,000 = 10\,500$ t at the beginning of 1981. This 1981 estimate compares well with hydroacoustic and spawning ground surveys which estimated 1981 biomass at approximately 9 000 t (Pacific Council 1981).

The SRA program was run using $M = 0.40$, $B_1 = 15\,000$ t and $P = 0.70$. This run indicated recruitment to be $R = 4\,909$ t, with 1973 to 1980 F values of 0.159, 0.435, 0.504, 0.297, 0.306, 0.277, 0.240, and 0.188, respectively.

PACIFIC HAKE, PORT SUSAN, 1966–81

Figure 3 shows the SRA plot for Pacific hake resulting from

TABLE 3. Catch data for Pacific hake in Port Susan (Kimura et al. 1981).

Year	Catch (t)
1966	2 865
1967	4 754
1968	3 703
1969	4 232
1970	4 087
1971	3 548
1972	1 895
1973	1 122
1974	2 285
1975	1 503
1976	1 396
1977	1 605
1978	3 031
1979	4 478
1980	4 490

analyzing the data in Table 3.

Hydroacoustic surveys in 1980 estimated population biomass at 12 156 t, while catch in 1980 was 4 490 t (Kimura et al. 1981). This high exploitation rate ($\hat{U} = 4\,490/12\,156 = 0.37$) gave the strong impression that the population was being overfished.

In the case of Pacific hake we have no independent estimate of initial biomass B_1, but we do have an estimate of 1980 biomass $B_{16} = 12\,156$ t (B_{16} is actually the biomass at the beginning of 1981). Therefore we work backward to find an estimate of B_1 and P which is consistent with the line of expected recruitment, and an estimate of $B_{16} = 12\,156$ t. Trying different combinations of B_1 and P, we find that when $B_1 = 18\,500$ t and $P = 0.70$, then $B_{16} = 12\,950$ t.

Although there is no obvious, simple interpolation to refine this solution, visual interpolation on Fig. 3, and a quick interactive computer session showed that $M = 0.65$, $B_1 = 17\,800$ t, and $P = 0.68$ is nearly an exact solution. For these values, $R = 8\,469$ t and F values for 1966 to 1980 are 0.243, 0.510, 0.457, 0.567, 0.577, 0.493, 0.232, 0.118, 0.233, 0.150, 0.134, 0.152, 0.307, 0.532, and 0.615, respectively.

Virtual Population Analysis (Kimura et al. 1981) indicated a 1966–69 biomass of between 10 297 and 16 828 t, somewhat less than the estimate using SRA.

With recruitment estimated to be 8 469 t, an annual catch of 4 490 t does not appear excessive. It appears that the hake population in Port Susan may not be a unit stock as was originally believed, but that recruitment might include a component of immigration.

Discussion

Starting with the basic SRA plot (the B_1 versus R relationship for a given P), it was found that the solution set could be reduced by adding the line of expected recruitment. We found that further application of ancillary information reduced the solution set to values useful in fishery management.

For Pacific ocean perch, our additional information was an analysis of CPUE data which indicated that $P = 0.25$; for Pacific herring the additional information was a hydroacoustic and spawning ground survey estimate of initial biomass $B_1 = 15\,000$ t; and for Pacific hake, the additional information was a hydroacoustic estimate of final biomass $B_{16} = 12\,156$ t. These three applications illustrate distinct ways in which SRA can be applied.

Although we have called the method Stock Reduction Analysis, it should be clear that the system of $n+1$ simultaneous equations could allow population biomass to increase (i.e. $P > 1$). In this case, and in other cases when B_1 does not represent virgin biomass, the expected recruitment line must also contain a component due to fishing mortality. If the population is in equilibrium, perhaps the line $R = B_1(1 - \exp(-F - M))$ would be appropriate, where F is an estimate of instantaneous fishing mortality in year 1. At any rate, the analysis is made more problematical.

An interesting property of the SRA plots (Fig. 1–3) is the apparent linearity of the B_1 versus R relationship for a given P. Although this appears to be a general rule the reason is not immediately apparent.

The principal weakness of SRA, as it is formulated here, is the assumption of constant recruitment. It is well-known that annual recruitment varies greatly in many marine fish species and when stocks have significantly declined it is probable that recruitment has also declined. We were pleased with our results using a constant recruitment model, and feel this success supports the belief that even when recruitment varies, a constant recruitment model may be adequate for explaining basic trends in abundance.

Nevertheless, SRA as presented here should be viewed as being most appropriate for short and medium length time series of catch data, while longer time series may be analyzed using Virtual Population type analyses (if age data are available). Because Virtual Population Analysis is most appropriate for long time series of data, SRA and Virtual Population Analysis complement each other.

Future research may show that it is possible to modify SRA to accommodate variable recruitment. A first attempt at analyzing such a catch series might be to break the time series in two at a point where recruitment was thought to change, and perform SRA on each half separately. Alternatively, a true variable recruitment model can be attempted.

In all of our analyses constant recruitment (Equation 2) was used. This is not an essential constraint and it appears probable that other recruitment relationships, which add only a single unknown parameter, might be acceptable. For example, recruitment could be proportional to biomass in the preceding year

$$(4)\quad B_i = B_{i-1}\exp(-F_{i-1} - M) + rB_{i-1} \qquad r > 0;$$

or proportional to some known set of constants

$$(5)\quad B_i = B_{i-1}\exp(-F_{i-1} - M) + rk_i \qquad 0 \le k_i \le 1.$$

Limited attempts trying equations (4) and (5) showed some promise for equation (5), but convergence problems for equation (4). The subject of generalizing SRA to handle variable recruitment is open to research.

We have found Stock Reduction Analysis to be a basically simple, effective tool to aid in the determination of stock condition. The method is adaptable, and could prove useful in many varied circumstances.

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Trophic Upsurge in New Reservoirs: A Model for Total Phosphorus Concentrations

Y. GRIMARD

Service de la qualité des eaux, Environnement Québec, 2360, chemin Sainte-Foy, Sainte-Foy (Québec) G1V 4H2

AND H. G. JONES

Institut national de la recherche scientifique-Eau, Université du Québec, 2700, rue Einstein, C.P. 7500, Sainte-Foy (Québec) G1V 4C7

GRIMARD, Y., AND H. G. JONES. 1982. Trophic upsurge in new reservoirs: a model for total phosphorus concentrations. Can. J. Fish. Aquat. Sci. 39: 1473–1483.

A model for total phosphorus concentrations during both the trophic upsurge and depression phases in new reservoirs has been developed by a convolution of the rate of phosphorus leaching from flooded lands and the rate of reservoir filling. Model parameters for phosphorus sedimentation and leaching coefficients were estimated from data available on the Smallwood Reservoir (impoundment 1971) in Labrador. The model was subsequently applied to predict phosphorus concentrations during the trophic upsurge phase in the La Grande-2 (LG2) Reservoir (impoundment 1978) in the James Bay region of Quebec. Because the sparse data available on other new or old reservoirs during the trophic upsurge phase does not permit an analysis of the confidence limits in model output, we include discussion of the calculated values of model parameters and their relationship to the real phenomena. An evaluation of the rates of phosphorus leaching from flooded soils and vegetation and the specific leaching coefficient of phosphorus from various lands has shown indirectly that the proposed model approximates the dynamics of new reservoir phosphorus concentrations. We conclude that the model has a good potential as an empirical predictive tool in the management of large new reservoirs on the Canadian Shield.

Key words: reservoir, phosphorus, model, trophic state

GRIMARD, Y., AND H. G. JONES. 1982. Trophic upsurge in new reservoirs: a model for total phosphorus concentrations. Can. J. Fish. Aquat. Sci. 39: 1473–1483.

Les concentrations de phosphore total durant la croissance de l'état trophique d'un réservoir après la fermeture du barrage et durant la régression subséquente de cet état sont décrites par un modèle ayant une solution analytique. Ce modèle est le résultat de la convolution du taux d'inondation des terres et du taux de lessivage du phosphore du sol inondé. Les valeurs des paramètres pour les taux de lessivage et de sédimentation pour le phosphore en suspension ont été déterminés à partir des données disponibles sur le réservoir Smallwood (fermeture du barrage en 1971), situé sur le bouclier canadien du Labrador. Par la suite, nous avons utilisé le modèle pour prédire les concentrations de phosphore pendant les périodes de croissance et de décroissance de l'état trophique pour le réservoir La Grande-2 (LG2; fermeture du barrage en 1978) dans la région de la baie James (Québec). En ce qui concerne les limites de confiance des résultats générés par le modèle, le manque de données disponibles sur d'autres réservoirs du bouclier canadien (après la fermeture de leurs barrages) ne permet pas un tel exercice. Par conséquent, nous avons surtout abordé l'étude des rapports entre les valeurs calculées pour les paramètres du modèle et les phénomènes réels. Une revue de la littérature démontre que le taux de lessivage du phosphore des terres inondées et de la quantité totale de phosphore disponible dans le sol et la végétation sont du même ordre de grandeur que ceux utilisés dans le modèle. Nous pensons donc que ce modèle reflète la dynamique réelle des réservoirs sur le bouclier canadien et, ce faisant, il peut être incorporé dans les processus de gestion des grands réservoirs comme un outil pratique et empirique de l'état trophique des réservoirs.

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ONE of the most significant environmental changes presently taking place on the Precambrian Shield area of eastern Canada is the creation of large artificial reservoirs for the production of hydroelectric power (Efford 1975; Baxter and Glaude 1980). Research projects on the impact of reservoir construction on both the terrestrial and aquatic ecosystems form a part of the current reservoir management programs (Lake Winnipeg, Churchill and Nelson Rivers Study Board 1971–75; Société d'énergie de la Baie James 1973–81). In the projects concerned primarily with the prediction of the changes in water quality, efforts have been directed towards the modeling of the trophic upsurge which follows the impoundment of the waters. This phenomenon, with its subsequent decline and return to a stabilized trophic state (trophic depression) has been well documented (Baranov 1961; Lowe-McConnell 1973; Rodhe 1964; Ostrofsky 1978). The trophic upsurge phase is caused by direct leaching and biological release of nutrients, particularly phosphorus, from the flooded vegetation and soil (Maystrenko and Denisova 1972; Campbell et al. 1976; Wilson et al. 1975). The trophic depression is the result of the exhaustion of the available nutrients from the flooded land and the gradual flushing of the reservoir towards a steady lake-type system.

Consideration of these facts led Ostrofsky (1978) to develop a conceptual model for the trophic changes in new reservoirs. This was achieved by the incorporation of a time-dependent expression for the leaching of phosphorus into the Vollenweider (1968) mass balance model of phosphorus for lakes. The Vollenweider model, which considers the lake as a continuously stirred tank reactor (CSTR), may be represented by the equation

$$(1) \qquad \frac{d[P]}{dt} = \frac{M}{V} - (\sigma + \rho)\,[P]$$

for which solution is:

$$(2) \qquad V[P] = \frac{M}{(\sigma + \rho)}\,(1 - e^{-(\sigma + \rho)t}) + V[P]_0\, e^{-(\sigma + \rho)t}$$

where $[P]$ is the concentration of total phosphorus in the lake waters at time (t) in $mg \cdot m^{-3}$, $[P]_0$ is the concentration of total phosphorus at time ($t = 0$) in $mg \cdot m^{-3}$, M is the annual total phosphorus loading of the lake in $mg \cdot yr^{-1}$, σ is the sedimentation rate coefficient in yr^{-1}, ρ is the flushing rate coefficient of the lake in yr^{-1}, and V is the lake volume in m^3. At steady state conditions (i.e. M constant and $t \rightarrow \infty$) equation (2) is reduced to

$$(3) \qquad V[P]_\infty = \frac{M}{(\sigma + \rho)}$$

From a study of the phosphorus leaching characteristics of vegetation and soil, Ostrofsky (1978) proposed that the amount of phosphorus (P_L, mg) leached into reservoir waters after impoundment could be represented by the equation

$$(4) \qquad \frac{dP_L}{dt} = \alpha P_F\, e^{-\alpha t}$$

Where P_F is the total phosphorus available in the flooded soil and vegetation in mg, and α is the leaching rate coefficient in yr^{-1} and $t = 0$ is the time of impoundment.

TABLE 1. Model parameter and variable input values for shield reservoirs.

Reservoir	Year of impoundment	Area of watershed km^2	Area of reservoir km^2	Area of flooded land (S_{max}) km^2	Annual phosphorus loading M/V, $kg \cdot yr^{-1}$	Phosphorus concentrations at time $t = 0$ $[P_w]$, $mg \cdot m^{-3}$	Flushing coefficient ρ, yr^{-1}	Sedimentation coefficient σ, yr^{-1}	ϕ, yr^{-1}	Flooding coefficient 'a', yr^{-1}	Leaching coefficient α, yr^{-1}	Specific phosphorus leaching coefficient K, $g \cdot m^{-2}$	aB $kg \cdot yr^{-2}$
Smallwood	1971	66.121×10^3	7.269×10^3	2.660×10^3	6.8×10^5	6.05	0.5	0.85	1.35	1	0.82	1.9	4.2×10^6
La Grande 2 (LG2)	1978	98.045×10^3	2.836×10^3	2.629×10^3	6.59×10^5	6.2	0.87	0.80	1.67	1.39	0.82	1.9	5.67×10^6
										1.39 (option 1)			4.7×10^6
La Grande 3 (LG3)	1981	65.683×10^3	2.461×10^3	2.176×10^3	4.42×10^5	5.8	0.66	0.66	1.32	0.69 (option 2)	0.82	1.9	2.34×10^6
										0.35 (option 3)			1.17×10^6

The rate of phosphorus leaching derived from equation (4) is then included in the Vollenweider CSTR model as a supplementary time dependent input. The new expression gives the equation:

$$(5) \quad \frac{d[P_w]}{dt} = \frac{M}{V} + \frac{B}{V}e^{-\alpha t} - (\sigma + \rho)[P_w]$$

for which the solution is:

$$(6) \quad V[P_w] = \frac{M}{\phi}(1 - e^{-\phi t}) + \frac{B}{(\phi - \alpha)}(e^{-\alpha t} - e^{-\phi t}) + V[P_w]_0 e^{-\phi t}$$

where $[P_w]$ is the phosphorus concentration in the reservoir at time (t) after impoundment in $mg \cdot m^{-3}$, $[P_w]_0$ is the calculated steady-state concentration of phosphorus in $mg \cdot m^{-3}$ in a hypothetical lake having the same morphological and hydrological characteristics as the reservoir, B represents the product of the leaching rate coefficient and the total phosphorus available in the flooded land (αP_F) in $mg \cdot yr^{-1}$, and ϕ is the sum of the sedimentation rate coefficient and the flushing rate coefficient ($\sigma + \rho$) in yr^{-1}.

Ostrofsky was not able to test his model in his study of the Smallwood Reservoir in Labrador (Churchill River watershed, impoundment 1971). However, from measured values of $[P_w]$ for 1975 and 1976, he used equation (6) to calculate values for α and B, and thus P_F, for the flooded land. If one subsequently takes these values of α and B to calculate the total phosphorus concentration of the Smallwood Reservoir waters in the first few years after impoundment (1971–74), very high values of $[P_w]$ are obtained (for t = 1 yr, $[P_w]$ = 121.8 $mg \cdot m^{-3}$; for t = 2 yr, $[P_w]$ = 61.9 $mg \cdot m^{-3}$). This is, of course, an exercise in tautology and cannot be used in any way as a test or validation of a model (Reckhow 1977; Golterman 1980). However, from the data of Duthie and Ostrofsky (1975), it can be concluded that the actual total phosphorus concentrations in the main water body of the Smallwood Reservoir in 1971–74 were far lower than those calculated by Ostrofsky's model. Equation (6), at least in this case may not have the power to generate total phosphorus concentrations close to the values of those present in the waters after impoundment.

Lewis and Nir (1978) pointed out in their work on the study of parameter estimation procedures that model equations must sufficiently represent the real system dynamics prior to any attempt to optimize parameters by algorithmic procedures. A relationship between the mathematical structure of model equations and the prominent dynamic phenomena of the systems they describe should be determined. In the case of the Ostrofsky Model, such an analysis shows that it assumes instantaneous flooding of the reservoir to the final volume. This, in turn, presumes the immediate start of the leaching process over the whole of the flooded area. In so far as the instantaneous filling of the reservoir is concerned, the conceptual basis of a CSTR model with constant ρ and σ precludes the inclusion of any time-dependent volume expression. However, the assumption that an apparent instantaneous flooding must dictate an immediate start to the leaching process over the whole of the flooded area, is not necessarily an inherent condition in such a model. It is possible to include, in a mass balance equation for a reservoir, an expression which describes the progression of the extent of the leaching process with time.

Large reservoirs may take from 2 to 3 yr to fill. The gradual increase in flooded surface over this time period should have a significant effect on the total phosphorus concentrations of the waters in the first few years after impoundment (Ostrofsky 1978). Our model was developed essentially to simulate more accurately this particular aspect of reservoir evolution. To make current applications of the model as practical as possible, we have expressed it as an analytical solution incorporating a number of fixed constants.

We report here results for the Smallwood Reservoir and the La Grande-2 (LG2) Reservoir (impoundment 1978) in the James Bay watershed. In addition, we illustrate the practical use of the model in reservoir management by demonstrating the influences that different filling rates will have on the trophic upsurge of the La Grande-3 (LG3) Reservoir (James Bay). This reservoir was impounded in April 1981.

Description of the Reservoirs

The Smallwood, LG2 and LG3 reservoirs are all large island-studded expanses of water lying along the same latitude in the Canadian Shield region of Eastern Canada (Table 1). The Smallwood Reservoir (53′5°N, 65°W) is the result of the impoundment (1971) of the Churchill River which flows into the North Atlantic at Hamilton Inlet on the Labrador coast. The LG2 Reservoir (53′5°N, 77°W, impoundment 1978) and the LG3 Reservoir (53′5°N, 76°W, impoundment 1981) were formed by the construction of dams and dikes in the La Grande River watershed (Société d'énergie de la Baie James — Société de développement de la Baie James 1974). This river flows into the eastern part of James Bay at Chisasibi (Fort George), Québec. Both watersheds are very similar in physiographic characteristics and may be best described as being a part of the taiga transition zone between boreal forest and tundra (Société d'énergie de la Baie James 1973–81). The zone is subjected to long cold winters and short mild summers. Mean annual temperature is −4°C with extremes of between −50 to 30°C (Ostrofsky 1978; Société d'énergie de la Baie James 1973–81). Mean annual precipitation is higher in the Smallwood region (84 cm) than that in the James Bay region (70 cm). Bedrock is Precambrian metamorphic gneiss and granite overlain with glacial deposits of silt, sand, gravel, and boulders. Ground cover consists mostly of *Larix laricana*, *Picea glauca*, and *P. mariana* with *Abies balsamea*, *Populus balsamifera*, *P. tremuloides*, and *Betula papyrifera* being concentrated along water courses and sheltered slopes facing south. Bogs and marshes are common to both areas although many more lakes have better defined shore lines in the James Bay region due to the sharper relief features of this area as compared to those on the Churchill River plateau (Ostrofsky and Duthie 1975). Due to the similarities between the bedrock and ground cover of the Churchill and La Grande River watersheds the chemical and phytoplankton characteristics of the natural waters of both regions are very similar (Ostrofsky and Duthie 1975).

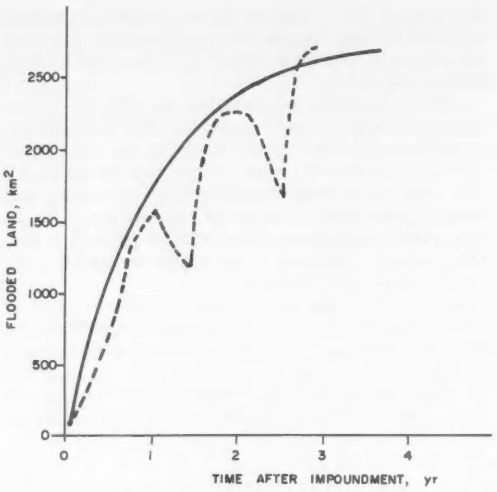

FIG. 1. The filling curve of the Smallwood Reservoir, Labrador. (– – – = measured filling curve 1971–75; ——— = curve derived from the expression $S = S_{max}(1 - e^{-at})$, ($a = 1$, $S_{max} = 2660$ km^2).)

Data

The data for the Smallwood Reservoir were taken from Ostrofsky (1978). The measured relationship between the area of flooded land and time after impoundment of the reservoir (filling curve) was supplied by Newfoundland Hydro (B. C. McGrath, Newfoundland Hydro, St. Johns, Nfld., personal communication 1980). All data for the LG2 and LG3 reservoirs were obtained from Société d'énergie de la Baie James (SEBJ, Service de l'Environnement, Place Dupuis, Montréal, Québec, personal communication 1980; Roy et al. 1980). For the LG2 reservoir, the mean concentrations of total phosphorus in the waters were compiled from the SEBJ data. The stations actually sampled were regrouped; each group of one or more stations was judged representative of a known flooded area of the reservoir during the filling process. As the reservoir filled, the number of groups gradually increased from two (2) at 0·0 yr to a maximum of eight (8) at 0·8 yr after impoundment. The mean phosphorus concentrations were then estimated by an area-weighted analysis of the contribution of each group of stations to the whole reservoir. The total phosphorus concentrations at each station were the values reported for integrated water samples. Each sample represented a water column extending to 10 m below the surface. The total phosphorus concentration recorded includes both the soluble and particulate forms (≤ 200 μm) of phosphorus.

The Model

In the development of the present model, the total flooded area of the reservoir is subdivided into an infinite number of parcels (ΔS_i). As each parcel becomes flooded it will release phosphorus according to the time dependent solution of equation (4). If the rate of surface flooding ($S'_{(t)}$) is known, it is then possible to calculate the total phosphorus released from each parcel at any point in time "t" after flooding commences. The resultant total phosphorus released during this time from all of the flooded land is the summation of that released by each parcel and may be expressed as:

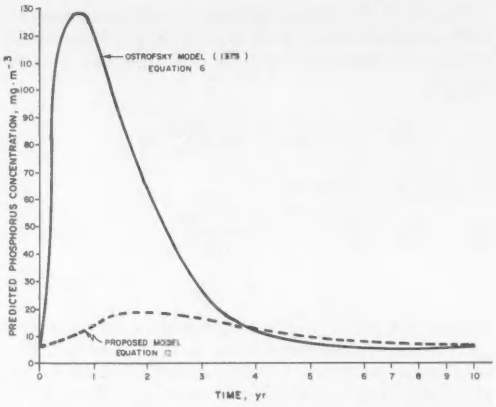

FIG. 2. Predicted phosphorus concentrations for the trophic upsurge and depression phases of the Smallwood Reservoir, Labrador.

$$(7) \quad P_L = \sum_{\Delta S_i} \frac{P_F}{S_{max}} \Delta S_i \, (1 - e^{-\alpha(t - t_i)})$$

where S_{max} is the total surface flooded in m^2, t is the flooding time in yr and t_i is the time (yr) at which flooding of ΔS_i occurred after the start of the flooding process.

If $\Delta S_i \to 0$, then the convolution of equation (4) with a rate of surface flooding ($S'(t)$) will give the following expression for the total amount of phosphorus (P_L) released after time (t)

$$(8) \quad P_L = \int_0^t K \, S'(t^*) \, (1 - e^{-\alpha(t - t^*)}) \, dt^*$$

where K is the specific phosphorus leaching coefficient (total phosphorus available from flooded soil and vegetation per unit surface area, P_F/S_{max}) in mg·m^{-2} and where both t, the actual time after impoundment, and t^*, the flooding time after impoundment, are in yr.

The rate of phosphorus release $\left(\frac{dP_L}{dt}\right)$ from the flooded land may be derived from equation (8) by applying the Leibnitz rule for the differentiation of an integral. This rate is then substituted for the term $Be^{-\alpha t}$ in equation (5) to give

$$(9) \quad \frac{d[P_w]}{dt} = \frac{M}{V} + \frac{1}{V} \int_0^t \alpha K \, S'(t^*) e^{-\alpha(t - t^*)} \, dt^* - (\sigma + \rho)\,[P_w]$$

for which the solution depends on the nature of $S'(t)$. This solution requires, a priori, that $S'(t)$ must be a continuous expression derived from the filling curve of a reservoir. In addition, the term $S'(t^*)e^{-\alpha(t - t^*)}$ in the rate expression for phosphorus release has to be capable of being integrated for $t \geq 0$.

To derive a continuous expression for the filling of the

reservoirs on the Canadian Shield, we have examined both the predicted hydrologic loading and morphometry of future reservoirs and the filling curves of existing reservoirs. Within the limitations created by the unique characteristics of each individual filling curve, we have found that an approximation of the general filling process may be written as

$$S = S_{\max}\,(1 - e^{-at}) \tag{10}$$

where S is the surface flooded at time (t) after impoundment in m^2, $S_{\max}$ is the surface flooded at the maximum operating volume of the reservoir in m^2 and 'a' is the flooding coefficient in yr^{-1}. Reservoirs in the Canadian Shield are generally formed by flooding glaciated U-shaped river valleys which gradually open out into rolling hills. We would thus expect the curve of equation (10) to closely reproduce those followed by the filling of reservoirs having this type of morphometry.

The rate of reservoir filling ($S'(t) = aS_{\max}e^{-at}$) derived from equation (10) is substituted in equation (8). The resulting expression can then be differentiated to give the rate of total phosphorus leaching during the filling of the reservoir $\left(\frac{dP_L}{dt}\right)$ as

$$\frac{dP_L}{dt} = a\,\alpha K\,S_{\max}\left(\frac{e^{-at} - e^{-\alpha t}}{\alpha - a}\right) \tag{11}$$

for $a \neq \alpha$.

$\alpha K\,S_{\max}$ may be reduced to the term B as $\alpha K\,S_{\max} = \alpha P_F = B$.

Equation (11) becomes the appropriate time dependent phosphorus input for substitution into equation (9). Equation (11) can also be integrated so that the solution of the substituted form of equation (9) is now given by

$$V[P_w] = \frac{M}{\phi}(1 - e^{-\phi t}) + \frac{aB}{(\alpha - a)}\left(\frac{(e^{-at} - e^{-\phi t})}{(\phi - a)} + \frac{(e^{-\phi t} - e^{-\alpha t})}{(\phi - \alpha)}\right) + V[P_w]_0 e^{-\phi t} \tag{12}$$

for $\alpha \neq \phi \neq a$. This is the model we propose for the mass balance of phosphorus in new reservoirs.

At the limit $a \to \infty$ equation (12) is reduced to equation (6) which is the Ostrofsky model. At the limit $a \to \infty$ and $t \to \infty$ equation (12) is reduced to equation (3) and the reservoir behaves as a lake under steady-state conditions as in the Vollenweider model.

Model Input (Table 1)

In addition to the appropriate measured data on phosphorus concentrations, other model input parameters were calculated as follows: 'a' was determined from a fit to measured filling curves using equation (10) and M was estimated from the morphometry of the La Grande watershed and the export coefficients of phosphorus for shield waters (Ostrofsky 1978). The value of ρ was calculated from the respective measured hydrologic loading of the LG2 or LG3 basin. $[P_w]_0$ and σ were calculated as follows (Ostrofsky 1978). As a first step, the phosphorus retention coefficient of the reservoir (R), was determined by applying the hydrologic loading model of Kirchner and Dillon (1975) to a hypothetical lake having the same value for qs (specific areal hydrologic loading) as the filled reservoir. Substitution of the value of R in the lake model of Dillon and Rigler (1974) gave $[P_w]_0$. $[P_w]_0$, which represents the theoretical steady state concentration of P in the reservoir with no leaching, is thus the equivalent of $[P]_\infty$ (equation (3)). σ is then determined from $[P_w]_0$ and equation (3). For LG2, $[P_w]_0$ was calculated to be 6.2 $mg \cdot m^{-3}$ and σ to be 0.8 yr^{-1} (Table 1).

Results

Smallwood Reservoir

The filling curve for the Smallwood Reservoir up to its maximum operating level is shown in Fig. 1. The two prominent minima at 1.5 and 2.6 yr after impoundment are the result of reservoir drawdown in the winter months. This is due both to the low hydrologic loading and the high discharge for hydroelectric production common to shield reservoirs during this period. A fit to this curve which respects both equation (10) and, as far as possible, the maxima of the filling curve is given by

$$S = 2.66 \times 10^9\,(1 - e^{-t})\,m \tag{13}$$

where the maximum flooded surface attained is 2660 km^2 (Table 1) and 'a', the flooding coefficient, is 1 yr^{-1}.

Substitution of this value of 'a' and the measured $[P_w]$ values for 1975 and 1976 into equation (12) permitted the estimation of α and B. The resulting value for α is 0.82 yr^{-1} and that for B is 4.2×10^{12} $mg \cdot yr^{-1}$. The values obtained by Ostrofsky (1978) and α and B using equation (6) are 1.5 yr^{-1} and 4×10^{13} $mg \cdot yr^{-1}$, respectively.

From the value of α, B, and $S_{\max}$, K is calculated to be 1.93×10^3 $mg \cdot m^{-2}$. Equation (12) is subsequently used to back calculate the values of $[P_w]$ for the period 1971–74 which represents the first 3 yr of impoundment. $[P_w]$ values were also calculated for the period from 1976 to 1981 inclusive. The resulting curve for the trophic upsurge and the trophic depression phases is shown in Fig. 2. A comparison of the values generated by the Ostrofsky model (equation (6)) with that of the present model (equation (12)) shows that the latter generates a curve having far lower values of $[P_w]$ for the trophic upsurge phase. On the other hand, the present model generates slightly higher $[P_w]$ values for the trophic depression phase. The Ostrofsky model situates the peak of the trophic upsurge ($[P_w] = 130$ $mg \cdot m^{-3}$) at 0.75 yr while that of the present model ($[P_w] = 18.6$ $mg \cdot m^{-3}$) is attained after 2 yr of impoundment. After 12 yr (1983) of impoundment, both models reproduce values of $[P_w]$ which, to all extent and purposes, are practically indistinguishable from one another (equation (6)) 6.06 $mg \cdot m^{-3}$; equation (12) 6.09 $mg \cdot m^{-3}$) and from the theoretical pre-impoundment value of $[P_w]_0$ (6.05 $mg \cdot m^{-3}$).

LG2 Reservoir (James Bay)

The diversion tunnels of the LG2 Reservoir were closed in November 1978. The filling curve of the reservoir (Fig. 3) shows the initial very slow filling rate during the winter months. The arrival of the spring runoff rapidly filled the

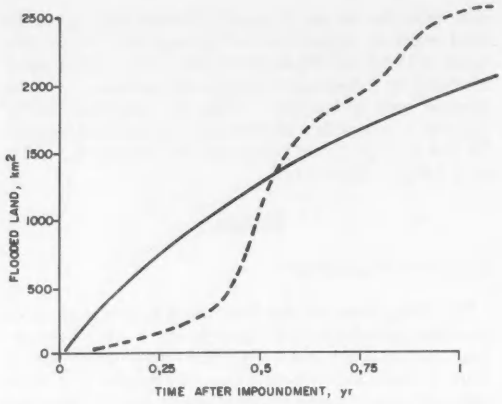

FIG. 3. The filling curve of the La Grande-2 (LG2) Reservoir, James Bay, Québec. (– – – = measured filling curve Nov. 1978–Nov. 1979; ——— = curve derived from the expression $S = S_{max}(1 - e^{-at})$, ($a = 1.39$ yr^{-1}, $S_{max} = 2629$ km^2).)

reservoir. To respect the complete filling curve, we have opted for the curve described by

$$(14) \quad S = 2.63 \times 10^9 (1 - e^{-2 \ln(2)t}) \text{ m}^2$$

The values of S from equation (14) coincide with those of the actual filling curve at $t = 0.5$ yr when the reservoir was half-full; it subsequently gives values slightly below those actually observed in the terminal stages of impoundment. $[P_W]$ values (Fig. 4) were calculated for the LG2 reservoir by equation (12) using the appropriate data from equation (14) and Table 1. As both the vegetation and the soil of the Churchill river and La Grande River watersheds are similar, the values of α and K used were those calculated for the Smallwood Reservoir. Figure 4 also reproduces the mean values for the phosphorus concentrations of the reservoir waters as estimated from the actual measured concentrations. The large standard deviations associated with these mean values reflect the heterogeneous distribution of the measured quantitites of total phosphorus $[P_W]$ in the reservoir waters during the filling of the basin and after the operating level had been reached. In the open-water periods for 1979 and 1980, the reservoir waters were susceptible to large scale turbulence due to the very deep thermocline (30 m) in 1979 and the absence of any well-defined thermocline in 1980 (Roy et al. 1980). Nevertheless, neither the vertical movement of the waters during the spring overturn or the wind-induced horizontal movements in summer succeeded in distributing the phosphorus released into the bottom waters evenly over the whole water column at any one time. The local release of phosphorus in bottom waters was appreciable. For example, in March 1980, the bottom waters of the flooded Kanaaupscow valley showed a total phosphorus concentration of 96 mg·m^{-3}, those over the old sediments of Lake Béréziuk, the largest lake to be flooded by the reservoir gave a total phosphorus concentration of 120 mg·m^{-3} while the concentration at the maximum depth (140 m) behind the dam at this time was 93 mg·m^{-3}. Although Fig. 4 shows the normal seasonal fluctuations associated with the total phosphorus cycle in lakes, the overall progression of the observed mean values parallels those predicted for the trophic upsurge phase during the first 2.5 yr after impoundment (winter 1978–79 to spring 1981). The actual values of the measured phosphorus concentrations during this period are consistently lower than those calculated by the model (ratio, predicted: observed conc. 1.03–2.02). As in the case of the predicted trophic upsurge, the overall progression of the measured concentrations seems to have passed a peak value of 16.8 mg·m^{-3} during the spring turnover in 1980 1.7 yr after impoundment. The peak value calculated for the LG2 Reservoir is 22.0 mg·m^{-3} at 1.6 yr after impoundment.

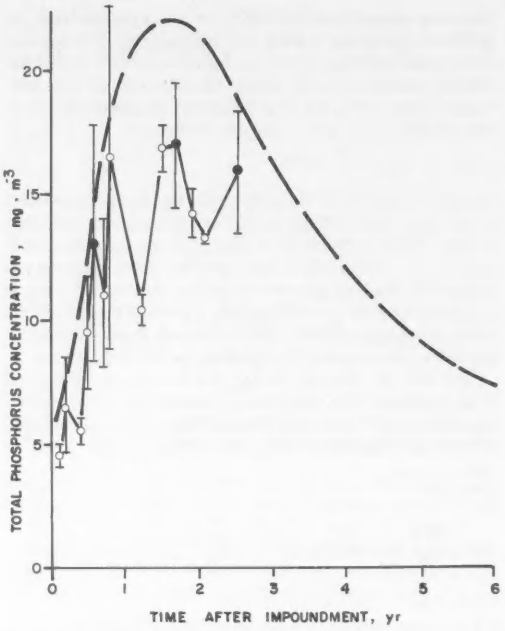

FIG. 4. Predicted and observed phosphorus concentrations for the trophic upsurge and depression phases of the La Grande-2 (LG2) Reservoir, James Bay, Québec. (– – – = predicted concentration (equation 12); ——— = area weighted mean values as calculated from measured values at all stations; ● = spring overturn concentration; ○ = epilimnetic (10 m) concentration.)

LG3 RESERVOIR

The dam for the LG3 Reservoir situated 112 km upstream from that of the LG2 Reservoir was closed in April 1981. From the morphometry of the reservoir and the hydrologic loading, we have simulated three possible options for the filling curve, equation (10), in which 'a', the flooding coefficient, has the value of 2 ln(2) yr^{-1} for option 1, ln(2) yr^{-1} for option 2 and 2^{-1} ln(2) yr^{-1} for option 3. S_{max} in all cases is 2.18×10^9 m^2. The trophic curves generated by the model from each of the filling options and the data in Table 1, are shown in Fig. 5. The values for α and K chosen for the LG3

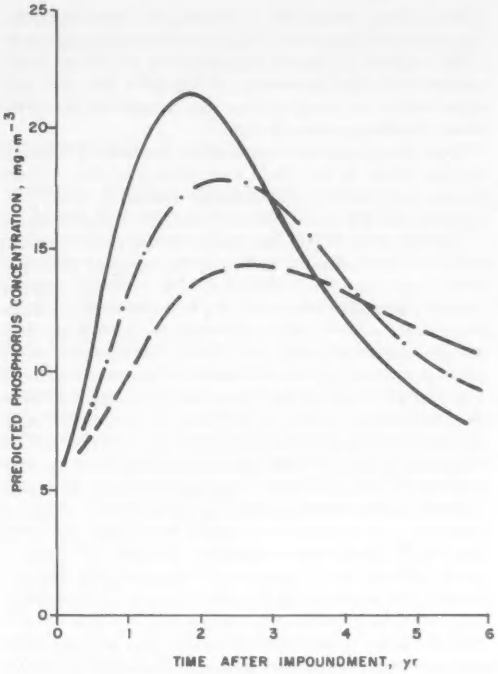

FIG. 5. Predicted phosphorus concentrations for the trophic upsurge and depression phases of the La Grande-3 (LG3) Reservoir, James Bay, Québec. (——— = filling option, flooding coefficient '*a*' 1.39 yr^{-1}; —·— = filling option, flooding coefficient '*a*' 0.69 yr^{-1}; – – – = filling option, flooding coefficient '*a*' 0.35 yr^{-1}.)

basin were those of the Smallwood Reservoir. Figure 5 demonstrates the influence of the filling process on the trophic upsurge of LG3. In effect, a fourfold reduction in the flooding coefficient, '*a*' from 2 ln(2) to 2^{-1} ln(2) results in a reduction of 32% of the expected peak concentration value of total phosphorus (21.5 $mg \cdot m^{-3}$, option 1; 14.6 $mg \cdot m^{-3}$, option 3). In addition, the maximum value of the phosphorus concentration of the slower filling process would be expected to peak one year later, in February 1984, than that predicted by the more accelerated filling curve.

Discussion

Model Structure

The model as described is a conceptual deterministic model with an explicit solution. It can be considered as a progression along one of two major pathways that the modeling of phosphorus has taken since the publication of the Vollenweider CSTR model (Chanuneau et al. 1980). Although the two pathways are closely related the first concerns the attempts that have been made to enlarge the conceptual base for lake models (Imboden 1973, 1974; Snodgrass and O'Melia 1975). The second direction is the development of the many empirical models based on the form of the Vollenweider conceptual model under steady state conditions, i.e. equation (2) (Dillon and Rigler 1974; Kirchner and Dillon 1975; Vollenweider 1975; Larsen and Mercier 1976 and Reckhow 1977). The proposed model is associated a priori with the development of models in which the conceptual base has taken into account the global dynamics of the system. However, the goal that the model be of practical use to water resource managers required that it be further developed as an empirical model. This desire to keep the model as simple and as practical as possible has led to a model which is a paradox. On one hand, its structure (equation (12)) includes the parameters ρ and σ for which the values are calculated for steady-state conditions. At the same moment in time the real reservoir is undergoing the dynamic changes of leaching and filling described by the nonsteady-state parameters α and '*a*'.

Paradox in the development of models is not necessarily a negation to their utilization as long as it is recognized (Patten et al. 1975). According to the time structure of the model, the reservoir theoretically never fills and the paradox is a permanent characteristic of the model. However, to all intents and purposes, the paradox will have a negligible effect on the use of the model in the later stages of the filling of the reservoir basin. This will be particularly true for the trophic depression phase as the asymptotic value for the phosphorus concentration is approached.

Model Confidence Limits

Because the model can be theoretically rejected as not representing the real evolution of a reservoir, it cannot be proved. It can, however, become the base for the development of an empirical model. This would be true if the conceptual model, in spite of its shortcomings, is an acceptable approximation of the real situation (Reckhow 1978). What constitutes an acceptable approximation of the real situation obviously depends on the projected use of the model and the confidence intervals allowed by the management in decision policy making.

As a first step in determining the confidence in the use of the reservoir model, we compared the data generated by the model to that obtained directly (LG2, Smallwood) and/or estimated (Smallwood) for the trophic upsurge and depression phases after impoundment. Our subjective appraisal of the data generated by the model equations for the reservoirs is that model output is acceptable as an approximation of the real system. The actual model output for LG2 becomes more acceptable if one only considers the relationship between predicted phosphorus concentrations and those observed during the spring overturn period (Fig. 4). Dillon (1975) has concluded that the total phosphorus concentration of lakes at spring overturn represents more accurately the true response of a lake to phosphorus loading than mean annual concentration. Considering that the major phosphorus input to a new reservoir is from the bottom waters and that the summer decline of epilimnetic phosphorus concentration is appreciable, we also believe that the spring overturn concentrations best represent the reaction of a reservoir to the annual allochthonous and autochthonous phosphorus loading. The term "acceptable," as used in the context of the above paragraph,

refers to the comparison between the observed total phosphorus concentrations at spring overturn and the predicted values. However, the subsequent steps to establish the confidence limits in the use of the model should be as objective as possible (Chapra and Reckhow 1979; Reckhow and Simpson 1980). Model error and model variable error should be estimated to permit the calculation of confidence limits. Reckhow and Simpson (1980) point out that the confidence limits should be strictly limited to systems similar to those from which the original model error was derived. In the case of the proposed model this causes a dilemma. In effect, large Shield reservoirs are few and far between compared to lakes in the same region. In the development of empirical lake models, data have been used from a large number of lakes; for example 13 lakes (Dillon and Rigler 1974; Kirchner and Dillon 1975), 20 lakes (Larsen and Mercier 1976), > 100 lakes (Reckhow 1977). In contrast, the whole area of the shield contains less than 25 reservoirs greater than 500 km^2 (Efford 1975). Four are presently under construction while only another 10 to 15 may be built within the next 15 yr.

In addition to the problem created by the restricted number of systems available for analysis, we have to consider that the data required must be obtained during the trophic upsurge and depression phases. At the present time, this type of data on the phosphorus dynamics of shield reservoirs is very rare (Baxter and Glaude 1980). The data used to develop the present model were taken from Ostrofsky (1978) and Société d'énergie de la Baie James (1973–81). The only other pertinent data on shield reservoirs are those of Hecky and Harper (1974) and Jackson and Hecky (1980) on the Notigi, Kettle, and Kelsey reservoirs in Manitoba.

The data of Jackson and Hecky (1980) on the Kettle Reservoir (Nelson River) would seem the most appropriate. This reservoir, impounded in 1971, was allowed to fill over a period of 2 yr (a = 1.2 yr^{-1}). The surface area is 333 km^2 of which 233 km^2 are flooded land. The reservoir is long and narrow (approx. 80 km × 4 km) with a very high flushing rate (ρ = 26 yr^{-1}). Phosphorus concentrations were measured from June 1972 to September 1974 for "backwater" (small protected bays) and "mainstem" (pelagic areas of almost river-like flow) regions of the reservoir. From the surface area of the reservoir and the depths of the sampling stations an estimate of the mean concentrations would be 28 $mg \cdot m^{-3}$ for 1972 (5 observations, June–October) and 25 $mg \cdot m^{-3}$ for 1973 (4 observations, June–October). The concentrations generated by the model (input: a = 1.2 yr^{-1}, ρ = 26 yr^{-1}, σ = 0.8 yr^{-1}, α = 0.82 yr^{-1}, $aB = 4.36 \times 10^{11}$ $mg \cdot yr^{-2}$) are 20.3 $mg \cdot m^{-3}$ and 21.7 $mg \cdot m^{-3}$ for 1972 and 1973, respectively. It would appear in this case that the model considers the reservoir to have been in the trophic upsurge phase for 1972 and 1973. In contrast the estimated mean concentrations from the measured data seem to indicate that the reservoir had already entered the trophic depression phase 2 yr after the impoundment. However, the results are far from conclusive. The error in the estimation of the mean phosphorus concentration could range from ±5 $mg \cdot m^{-3}$ (1972) to ±6 $mg \cdot m^{-3}$ (1973). In addition Jackson and Hecky (1980) report phosphorus concentrations of 41.6 $mg \cdot m^{-3}$ (mainstem) and 163 $mg \cdot m^{-3}$ (backwater) for September 1974 which would indicate that the reservoir was still in the trophic upsurge phase. However, only one observation was recorded in that year. One should note that Jackson and Hecky (1980) reported values for total dissolved phosphorus in the samples after filtration through a filter of 1 μm. The estimated values may thus be lower than the true values for the mean phosphorus concentrations.

Some phosphorus data available on reservoirs in climatic regions similar to the shield have been published by both Russian and Scandinavian workers. Denisova (1978), reviewed the long-term changes in the nutrient concentrations of the Dnieper River before and after the filling of the Kakhova Reservoir (impoundment 1956), the Kremenchug Reservoir (1961), and the Kiev Reservoir (1965). These are shallow nonstratified water bodies with very high renewal rates (Kiev Reservoir, ρ = 9–12 yr^{-1}). Although Denisova draws general conclusions regarding the leaching of the soil and the input–output budgets for phosphorus in the reservoirs, it is very difficult to obtain any idea of the quantitative relationship between the two phenomena. Both the phosphorus input and output were correlated with total annual flow. The net measured retention of phosphorus can be negative or positive in alternate years and no continuous trophic upsurge or trophic depression phases are apparent. In so far as the model is concerned, it would be very difficult to estimate 'a' as no detail on the filling of the reservoirs are given. It should be noted, however, that the spring runoff in this region could fill these shallow reservoirs in 2–3 wk. In contrast, the Rybinsk Reservoir (Sorokin 1972) on the Volga (ρ = 1.4 yr^{-1}, V = 25 × 10^9 m^3) is more similar to the deeper eastern Canadian reservoirs than those on the Dnieper. Unfortunately, no phosphorus data are available on the reservoir during its early years (impoundment 1941). Rodhe (1964) has studied the chemical and plankton dynamics of the Ransaren Reservoir (impoundment 1957) in Swedish Lappland (latitude 65°N). The climatic regime, the ground cover and the water quality of the region closely resembles those of the eastern Canadian Shield. The reservoir filled very rapidly in the spring and summer of 1957 (a = 6 yr^{-1}). From the published data, and an estimation of the land flooded from the original lake–reservoir depth relationship, the model predicts that the reservoir would have peaked through the trophic upsurge phase in the 1st yr (1958 $[P_w]$ = 13.0 $mg \cdot m^{-3}$). The mean value for the 2nd full yr after impoundment (1959) is calculated to be 10.9 $mg \cdot m^{-3}$. The actual total phosphorus concentrations estimated from the reported data of Rodhe (1964) are 6.5 $mg \cdot m^{-3}$ for 1958 and 9.5 $mg \cdot m^{-3}$ for 1959. The reason for the large difference between the estimated and predicted phosphorus concentrations in the first full year after impoundment is the large fluctuations in water level. The level of the reservoir was reduced considerably below that of the original lake in the winter drawdown of 1957–58. It was refilled again with snow-melt runoff in the spring of 1958. The phosphorus concentrations therefore, reflect more the quality of the input at this time than the leaching from the flooded land.

This limited number of case studies to which we can apply the reservoir model reduces the confidence in this particular model as opposed to the now well established confidence in lake models (Reckhow and Simpson 1980). We cannot, however, give a detailed analysis of the actual confidence limits

as the data base is so sparse. A contribution can be made, however, to establishing a certain confidence in the use of the reservoir model by evaluating the credibility of the values, either measured or predicted, of certain of the individual model parameters.

Model Parameter Values

Both ρ, the flushing coefficient, and '*a*', the flooding coefficient, may be measured or estimated from the hydrological and morphological characteristics of the reservoir and of all the constants used in operating the model, the ones for which the values are thus the most reliable.

On the other hand, σ, the sedimentation rate coefficient, is extremely difficult to measure directly in real systems. In effect, lake empirical models owe their development to the difficulty of obtaining independently measured values of σ for the proof of the Vollenweider (1968) conceptual model. The conceptual link-up between the empirical models and that of Vollenweider implies that the values of σ lie within a narrow range for similar-type lakes at steady state. They can then virtually be considered as being "constant." Such a model is the empirical model of Kirchner and Dillon (1975) for the phosphorus retention of lakes.

Some preliminary data on the large lakes in the LG2 region (i.e. Lake Bérériuk, Lake Coutaceau) prior to flooding show that the application of the Kirchner and Dillon (1975) model to these lakes produced results close to those reported by the authors for lakes with similar areal loadings. The water quality input to the LG2 Reservoir is very similar to the surrounding lakes and it was thus decided to maintain the use of the Kirchner and Dillon model to calculate $[P_w]$ (6.2 mg·m^{-3}) and σ (0.8 mg·m^{-3}).

During the filling of the LG2 Reservoir in the winter of 1978–79, there was no outflow from the reservoir. If a reservoir receives a constant hydrological input (Q_i) with a phosphorus concentration of $[P_i]$ then one can calculate the value of σ from the expression:

$$(15) \quad [P_w] = \frac{1}{t}\frac{[P_i]}{\sigma}(1 - e^{-\sigma t})$$

where $[P_w]$ is the concentration of phosphorus in the reservoir at time t[1].

The reservoir LG2 was allowed to fill during the winter season of November 1978 through to June 1979. If we assume that under the ice cover and with low levels of turbulence in the water column there is very little diffusion of released phosphorus from the bottom upwards then the values of $[P_w]$ of the top waters should permit one to calculate σ by equation (15). In May 1979 (0.5 yr) after impoundment and before ice-off the mean concentration of phosphorus in the top waters of the reservoir (10 m) was 9.5 mg·m^{-3}. Substitution of this value equation (15) gives a solution for σ of 1.03 yr^{-1}. However, this would be a minimal value for σ as we know that leaching did occur. In the subsequent spring turnover the overall mean concentration of phosphorus in the reservoir was 13.2 mg·m^{-3}. In addition, the flow was not constant. A volume-weighted average stagnation time of water in the reservoir would be shorter than the time from the closure of the flood gates due to the different volume contributions of winter flow and the subsequent spring runoff. However, the relative values of σ as calculated from the Kirchner and Dillon empirical model and the filling of LG2 can be considered as close particularly if one examines other possible sources of error in quantifying all the model variable inputs.

In order to determine the relationship between the value of α, the leaching rate coefficient used in the model and any "real" rate of phosphorus release from flooded land, one has to estimate the latter by indirect means. Such estimations may be made from controlled laboratory, or "in situ," studies on the release of phosphorus from different types of organic substrates immersed in water.

Maystrenko and Denisova (1972) and Gunnison et al. (1980) have studied nutrient release from flooded soils. Maystrenko and Denisova (1972), in a laboratory simulation of the flooding of the Dnieper River plain monitored the release of organic matter and nutrients from different types of flooded soils. From their data a calculation of α for phosphorus release at temperatures of between 7 and 23°C for peaty, chernozem, clayey and sandy soils gives an average value of 4.4 yr^{-1}. It should be noted that the form of phosphorus measured in these experiments was total dissolved mineral phosphorus. Gunnison et al. (1980) who studied the phosphorus release from Minnesota alluvial soil under successive aerobic and anaerobic conditions, found the rate of total phosphorus release to be 0.03 d^{-1}; i.e. α = 11 yr^{-1}. This rate represents the overall microbiological release of phosphorus from the organic substrates in the soil at 20°C. In large shield reservoirs, release rates will be lower due to cold bottom water (4°C). Only in the brief summer periods, during which the maximum temperature of the epilimnetic waters can come close to 20°C (15–17°C), will phosphorus release rates in shallow waters approach those reported by Gunnison et al. (1980) or by Maystrenko and Denisova (1972). If one assumes that the relationship between community microbial activity and temperature is of an exponential nature (equation of Hargrave 1969), then the value of α at a mean annual temperature of 5–7°C would be from 2 to 3 yr^{-1} for soils similar to those studied by Gunnison et al. (1980) to 1–1.5 yr^{-1} for the peaty and sandy type of soils reported by Maystrenko and Denisova (1972). The soil cover on the shield is not composed of much alluvial soil but consists rather of podzol and associated bog soils with high humic content. Humic materials are known to bind phosphorus strongly (Jackson and Schindler 1975) and the difference in value of α between the peaty type and alluvial soils may be due to the higher quantity of humic materials found in peat and bog soils. In the alluvial soils the faster release of phosphorus is thus associated with its greater availability to decomposer organisms as compared to the more refractory nature of phosphorus in peat and bog soils.

Smith (1981) carried out long-term leaching studies on subarctic bog soils which are more similar to those on the shield than alluvial soil. In this study phosphorus was not

[1]The derivation of this equation is based on the supposition that the rate of total phosphorus sedimentation is a function of the phosphorus concentration in the water column. This hypothesis was first used by Vollenweider (1968) in the derivation of the model for phosphorus concentration in lakes.

measured as a water quality parameter. However, the concomitant release of iron and humic matter (color) from a grass bog-spruce transition soil gave an estimated value of 0.7 yr^{-1} for these parameters at a mean temperature of 4°C. This value could reflect the approximate rate of release for those forms of phosphorus closely associated with these materials in both soil and water.

From the above discussion, it would seem that the value for α for shield reservoirs could fall anywhere in the range of 0.7–3 yr^{-1}. The value of α (0.82 yr^{-1}) used as model input was calculated from the data on the Smallwood reservoir. This value falls well within the range for the possible values of α as estimated by the other means. This warrants a certain degree of confidence in the model as it can now be considered to represent approximately the quantitative dynamics of the systems.

In the solution for α, B, and K are obtained simultaneously. For the Smallwood reservoir, the value of K obtained by this method is 1.9 $g \cdot m^{-2}$. This is the value which was subsequently used in the model to predict the phosphorus concentrations in the LG2 reservoir.

An independant measure of the leachable phosphorus content is necessary. It should then be possible to determine how relevant the value of K, calculated by the model, is to the actual phosphorus released from the flooded land. One should note that K is the net leachable phosphorus content per unit area of the flooded soil and associated vegetation. Phosphorus forms that are released and then resedimented back to the bottom soil without being distributed throughout the water column are not covered by this term.

From the data of Gunnison et al. (1980), one can calculate a value of K of 1.3 $g \cdot m^{-2}$ for Minnesota alluvial soils. As the experimental method does not take into account any resedimentation of the released phosphorus, this value is directly related to K of the model. Maystrenko and Denisova (1972) have estimated K values for flooded soils of the Dnieper flood plain. The value (K = 0.07 $g \cdot m^{-2}$, for meadow alluvial soils) is lower than that calculated from the data of Gunnison et al. (1980). In the case of peaty and sandy soils, K values of 0.02 $g \cdot m^{-2}$ may be calculated from Maystrenko and Denisova's (1972) data. These would only be approximate true K values as the figures refer to the totality of the phosphorus released over a 1-yr period.

The actual amount of phosphorus leached from the vegetation is related to the type and distribution of the ground cover flooded. From the empirical coefficients of phosphorus release given by Maystrenko and Denisova (1972) from forest and meadow vegetation, and an estimation of the biomass distribution of such materials in lands similar to those flooded in the Smallwood and LG2 reservoirs (100–125 $t \cdot ha^{-1}$, Rodin et al. 1975), approximate values of between 0.96 and 6.88 $g \cdot m^{-2}$ of leachable phosphorus can be calculated. It would thus seem from the results of these authors that the microbiological release of the high energy forms of phosphorus found in low ground cover vegetation rather than direct leaching of soil would be the major contributor to the final release of phosphorus into the water column of new reservoirs. However, the test materials of Maystrenko and Denisova (1972) were dried and ground prior to flooding. This experimental procedure would overestimate the potential amount of leached phosphorus, at least in the time period (1 yr) quoted by these authors. Although it is thus difficult to determine exactly the true value of the potential leachable phosphorus content of the flooded lands, the value for K (1.9 $g \cdot m^{2}$) used in the model for the LG2 reservoir would seem to be of the same order as those values calculated from the literature for soil and associated biomass.

Summary

In conclusion, the model as defined bears some promise as the base for an empirical model although compatible data on reservoir systems are rare. However, confidence in the model is enhanced as the values of certain model parameters (σ, α, and K) are of the same order of magnitude as those calculated by independant means. The model was developed as a simple analytical solution incorporating these parameters as constants calculated from the data on the Smallwood Reservoir. We acknowledge, however, that an empirical optimization of these parameter values from the phosphorus concentrations for the LG2, the LG3 and other shield reservoirs under construction (LG4, Caniapiscau, the Nottaway, Broadback, and Rupert rivers hydroelectric complex) will probably lead to values for α and K which are more representative of all shield reservoirs.

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Descriptions and Keys for Ammocoetes of Lampreys from British Columbia, Canada

J. E. RICHARDS[1]

Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1

R. J. BEAMISH

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

AND F. W. H. BEAMISH

Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1

RICHARDS, J. E., R. J. BEAMISH, AND F. W. H. BEAMISH. 1982. Descriptions and keys for ammocoetes of lampreys from British Columbia, Canada. Can. J. Fish. Aquat. Sci. 39: 1484 – 1495.

Characters useful for the identification of ammocoetes of lampreys found in British Columbia were verified by rearing ammocoetes through metamorphosis to specifically identifiable adults. We developed a key that employs new as well as some previously published features. We showed that published descriptions previously thought to be characteristic of species are unreliable for taxonomy. Counts of trunk myomeres and body proportions were not useful for separating species.

Key words: ammocoetes, taxonomy, identification criteria

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En élevant des ammocètes jusqu'au stade adulte identifiable, en passant par la métamorphose, il a été possible de vérifier les caractères taxonomiques des ammocètes de lamproies rencontrées en Colombie-Britannique. Nous avons préparé une clé reposant sur des caractères à la fois nouveaux et déjà publiés. Nous démontrons que des diagnoses jadis considérées comme étant caractéristiques de l'espèce ne sont pas fiables en taxonomie. Les comptages de myomères du tronc et les proportions du corps ne permettent pas de séparer les espèces.

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LAMPREYS are probably present in most coastal rivers and streams in British Columbia, but little is known about the relative abundance of the various species. There are two anadromous species, the Pacific lamprey, *Lampetra tridentata*, and the river lamprey, *Lampetra ayresi*, and one freshwater parasitic species, *Lampreta macrostoma* (Beamish 1982). All are parasitic on commercially important fishes. One nonparasitic lamprey, *Lampetra richardsoni*, is also widely distributed throughout British Columbia. Observations on the relative abundance of adults in saltwater and returning to spawn in freshwater (Beamish 1980) indicate that the Pacific lamprey is the most abundant of these parasitic lampreys and poses the most serious threat to other fishes.

To assess the impact of lamprey attacks on commercial fishes it is necessary to estimate the abundance of the parasitic species. Initially these estimates can be very approximate, but it is important to know the order of magnitude of lamprey abundance in the various watersheds. Juvenile anadromous lamprey can be specifically identified but it is both technically difficult and expensive to enumerate them during this period. During the larval period, when ammocoetes live burrowed in the mud and sand of the stream bed, they are susceptible to electrofishing and large numbers can be collected; it is during this time that abundance data are easiest to obtain. In preliminary studies Richards (1980) concluded that identification of ammocoetes using published criteria is unreliable. Therefore it was necessary to reevaluate taxonomic criteria for the identification of ammocoetes found in coastal streams of British Columbia. The establishment of reliable characters

[1]Present address: Ministry of Environment, Marine Resources Branch, Victoria, B.C. V8V 1X5.

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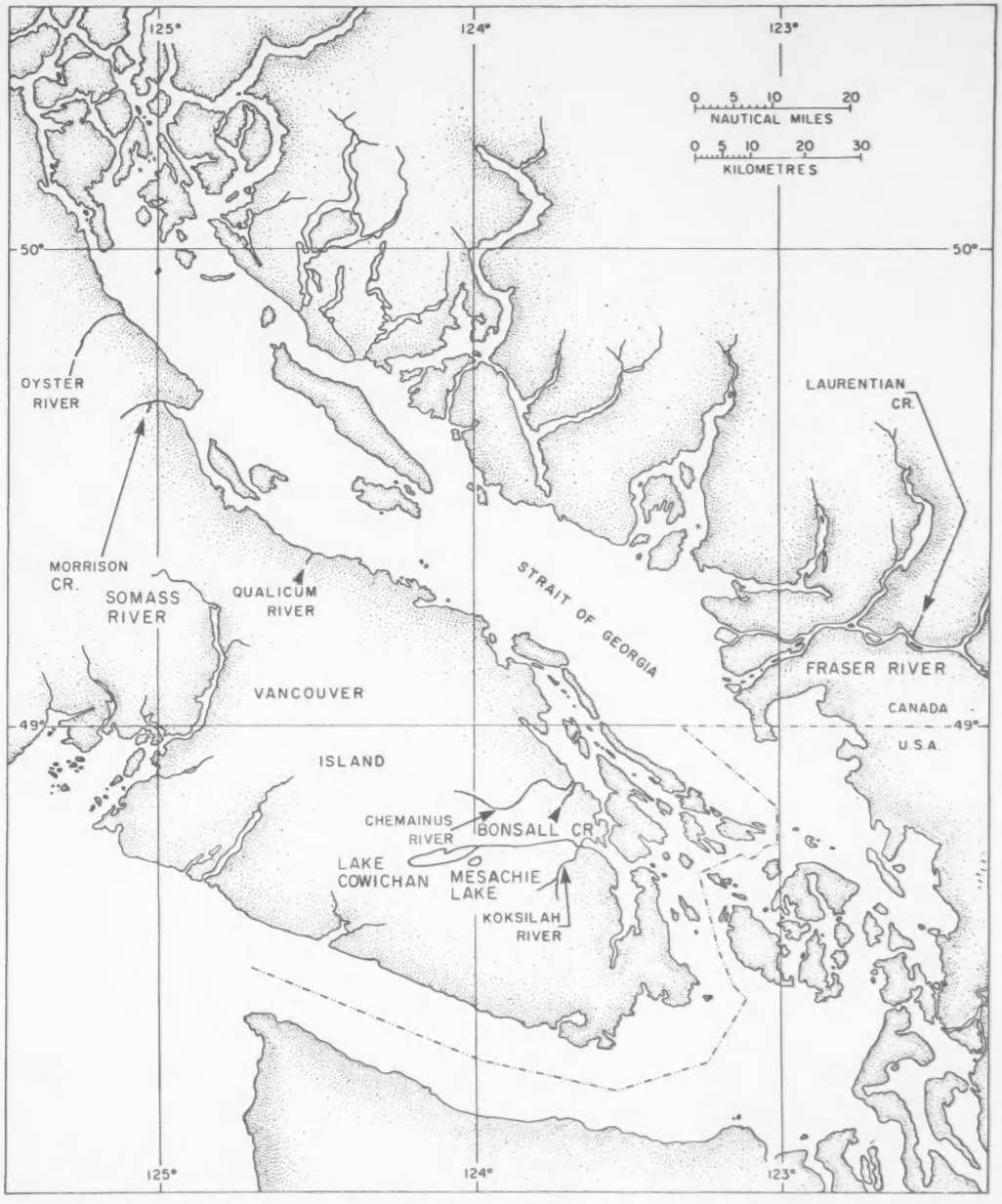

FIG. 1. The lower coast of British Columbia showing the locations of streams where samples of ammocoetes were collected.

required the rearing of ammocoetes to verify the species to which they belonged.

This paper reviews and revises the taxonomy of lamprey ammocoetes in British Columbia. A key is presented that uses characters that are confirmed as being taxonomically significant at the species level.

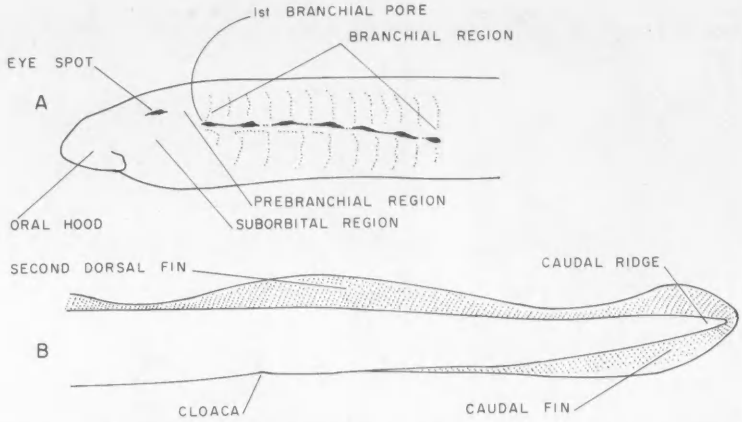

FIG. 2. Drawing of a typical ammocoete showing the external regions used to describe pigmentation patterns (Vladykov 1950). A) Head region, B) Tail region.

Materials and Methods

Most ammocoetes were collected by electrofishing from sites in rivers that were within 5 km of the tidal boundary (Fig. 1). One sample was obtained from Laurentian Creek which enters the Fraser River 30 km from the ocean. Ammocoetes were also collected from a dredging operation in the Fraser River near Mission, British Columbia, 65 km from the mouth of the river. All samples were transported live to the laboratory, anesthetized with tricane methane sulfonate (MS222), measured for total length, and examined for external morphological characteristics. Most were then preserved in 5% formalin and subsequently reexamined. Subsamples of ammocoetes from some collections were held alive in 375-L rearing tanks. The tanks contained a substrate of fine washed sand and were supplied with running dechlorinated fresh water of ambient temperature that fluctuated seasonally from 6 to 20°C. Ammocoetes were fed twice weekly following the procedures of Hanson et al. (1974) until metamorphosis was complete. Metamorphosed lampreys were transferred from freshwater (0‰) to full strength sea water 28−30‰ over a 3-d period to determine if they were *L. ayresi* which can survive in salt water or *L. richardsoni* which cannot.

External pigmentation pattern from various body regions (Fig. 2; Vladykov 1950) was described for both fresh and preserved material.

Pigmentation of the tongue precursor was examined and described following the methodology of Vladykov (1950). The number of trunk muscle myomeres was determined by removing a strip of skin from the left side of the ammocoete and counting the myomeres between the posterior branchial pore and the cloaca (Hubbs and Trautman 1937). The first myomere counted was the one that contained no portion of the last branchial pore and the last myomere was the one whose lower posterior angle lies in part or wholly above the cloacal slit. In some cases the muscles were stained with eosin (Pletcher 1963) to enhance differentiation of the myomeres and myoseptae. Samples of 203 *L. tridentata*, 254 *L. richardsoni* and 50 *L. ayresi* were examined for tongue precursor pigmentation patterns and the number of trunk myomeres.

Body proportions were measured to the nearest 0.1 mm from the left side of the ammocoete using the following definitions from Hubbs and Trautman (1937) and Vladykov (1950): Prebranchial length, tip of snout to the anterior edge of the first branchial pore; branchial length, the anterior edge of the first branchial pore to the posterior edge of the last branchial pore; trunk length, the posterior edge of the last branchial pore to the anterior edge of the cloaca; tail length, the anterior edge of the cloaca to the posterior edge of the caudal fin; total length, the tip of the snout to the posterior edge of the caudal fin. The dentition of postlarval lampreys was examined using a dissecting microscope, and described according to the terminology and definitions which follow Vladykov and Follett (1967).

To establish the size at which pigmentation differences could first be distinguished, we reared *L. ayresi* and *L. richardsoni* ammocoetes from eggs that were fertilized in the laboratory. Eggs were held in trays and floated in tanks containing running dechlorinated water of ambient temperature. Prolarvae were transferred to tanks containing sand substrate and reared on a diet of algae and yeast. During the rearing period, samples of these ammocoetes were collected from the tanks after 3, 12, and 24 mo, then anesthetized and examined for pigmentation pattern. Reared *L. ayresi* ammocoetes were maintained for 2 yr and *L. richardsoni* ammocoetes for 1 yr.

Results

LAMPETRA TRIDENTATA

A sample of 41 ammocoetes (length range 96−144 mm) from the Qualicum River (Fig. 1) collected in July 1977 was identified as *L. richardsoni* on the basis of the pigmentation pattern of the anterior region as described for preserved speci-

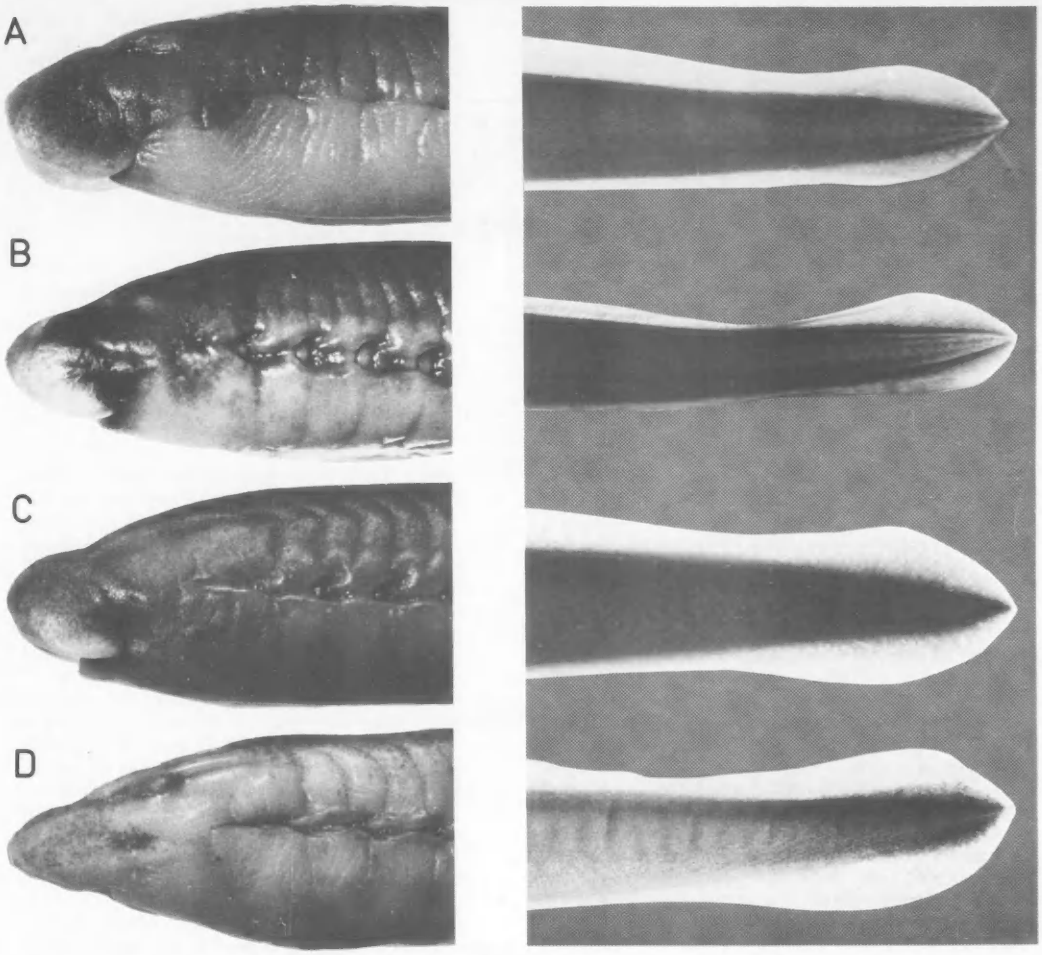

FIG. 3. Head and tail pigmentation of (A) *L. tridentata*, (B) *L. macrostoma*, (C) *L. richardsoni* and (D) *L. ayresi*. Note the light caudal ridge of the *L. tridentata* and *L. macrostoma* ammocoetes, dark tail of *L. richardsoni* and the intermediate condition of *L. ayresi*. The head of *L. ayresi* is more lightly pigmented than the other species. The pattern of pigmentation in the head region of *L. tridentata*, *L. macrostoma* and *L. richardsoni* represents the average condition observed in this study.

mens by Vladykov and Follett (1965) and Pletcher (1963). The ammocoetes were kept alive and in February 1978, six had metamorphosed. The dentition of these postlarval individuals clearly indicated they were *L. tridentata* and not *L. richardsoni*. These observations and the discrepancies between the descriptions of Vladykov and Kott (1976a) and Pletcher (1963) of the head pigment patterns of *L. tridentata* ammocoetes indicated that head pigmentation as previously described may not be suitable for separating *L. tridentata* ammocoetes from other species.

Reexamination of the external pigmentation of live as well as preserved specimens collected from various streams revealed two distinctly different tail patterns associated with the posterior termination of the notochord in the caudal fin. The termination of the notochord and overlying tissues form a lateral thickening in the tail region and will be referred to as the caudal ridge (Fig. 2).

The specimens in the Qualicum River sample (now shown to contain at least some *L. tridentata* ammocoetes) were reexamined and all were observed to possess a common pigmentation pattern in the tail region. The caudal ridge was lightly pigmented, surrounded by a border of much darker pigmentation which uniformly faded to a light grey towards the peripheral margins of the caudal fin (Fig. 3A). An

TABLE 1. Body proportions of *L. tridentata* ammocoetes from various streams in British Columbia. Values expressed in percent total length ±1 SD.

	Total length (mm)												
	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149
Number	3	3	16	15	16	5	18	21	47	41	29	23	5
Prebranchial													
Qualicum	—	—	—	—	—	—	9.6±1.4	8.5±0.4	8.3±0.4	8.3±0.4	7.6±0.5	7.5±0.4	6.8±0.2
Oyster	13.0±0.5	12.1	11.2±0.8	10.3±0.5	9.7±0.2	—	—	8.5±0.3	8.0±0.4	7.8±0.4	7.6±0.2	7.3±0.3	6.9
Koksilah	—	—	—	—	—	—	—	8.6	8.7±0.2	8.1±0.1	8.1±0.4	7.8	–
Chemainus	—	11.6±0.5	10.8±0.3	10.2±0.2	9.7±0.3	9.5±0.3	8.7±0.4	8.5±0.4	8.3±0.4	8.0±0.1	7.6	—	–
mean	13.0	11.8	11.0	10.2	9.7	9.5	9.1	8.5	8.3	8.0	7.7	7.5	6.8
Branchial													
Qualicum	—	—	—	—	—	—	12.6±0.2	12.4±0.6	12.8±0.5	12.1±0.6	11.7±0.5	11.9±0.3	10.6±0.2
Oyster	15.8±0.6	15.0	14.3±0.1	13.8±0.4	13.2±0.1	—	—	13.1±0.5	12.7±0.6	12.4±0.6	12.0±0.3	12.1±0.6	11.4
Koksilah	—	—	—	—	—	—	—	12.7	12.9±0.4	12.5±0.4	12.2±0.4	11.7	–
Chemainus	—	14.4±0.7	14.2±0.6	12.8±0.7	13.6±0.8	13.2±0.3	13.3±0.5	12.7±0.6	12.7±0.6	12.3±0.6	11.4	—	–
mean	15.8	14.7	14.2	13.8	13.4	13.2	12.9	12.7	12.8	12.3	11.8	11.9	11.0
Trunk													
Qualicum	—	—	—	—	—	—	49.8±0.2	49.6±0.8	49.9±0.2	50.0±0.8	50.9±0.9	50.2±0.8	51.2±1.1
Oyster	55.3±1.5	53.5	50.7±0.5	50.1±1.8	49.5±1.2	—	—	50.2±0.8	51.0±1.1	50.2±1.2	50.5±1.1	50.6±1.2	52.1
Koksilah	—	—	—	—	—	—	—	48.5	49.0±0.6	49.4±0.9	48.8±0.7	49.2	–
Chemainus	—	49.5±0.3	50.5±1.8	49.4±0.9	49.4±1.0	49.7±0.4	50.0±0.8	49.6±1.3	49.6±0.9	49.1±0.8	50.1	—	–
mean	55.3	51.5	50.6	49.7	49.4	49.7	49.9	49.5	49.9	49.7	50.1	50.0	51.6
Tail													
Qualicum	—	—	—	—	—	—	28.2±0.7	29.3±0.9	29.1±1.3	29.9±1.3	29.7±1.3	30.1±0.6	30.7±0.9
Oyster	18.4±0.8	22.9	24.6±0.3	26.0±1.1	26.7±0.2	—	—	28.6±0.2	29.0±0.8	30.1±1.2	30.0±0.6	30.2±0.7	29.4
Koksilah	—	—	—	—	—	—	—	29.6	29.8±0.3	29.8±0.9	30.8±0.5	31.3	–
Chemainus	—	23.0±1.3	24.8±1.5	25.9±1.1	27.2±0.8	27.9±0.3	28.5±0.9	29.8±1.1	30.9±0.8	30.3±1.0	30.5	—	–
mean	18.4	22.9	24.7	25.9	26.9	27.9	28.3	29.3	29.5	30.0	30.2	30.5	30.3

TABLE 2. Muscle myomere counts for ammocoetes of *L. richardsoni*, *L. tridentata*, and *L. ayresi* from several streams in British Columbia (±1 SD).

Species	Location	Sample size	Number of myomeres												Mean ± SD
			58	59	60	61	62	63	64	65	66	67	68	69	
L. richardsoni	Oyster R.	108	2	2	11	23	33	27	7	2	1	—	—	—	61.9±1.4
	Morrison Cr.	78	—	—	—	10	13	31	17	4	2	1	—	—	63.0±1.2
	Bonsall Cr.	25	—	—	—	—	—	5	6	5	7	2	—	—	64.8±1.3
	Koksilah R.	26	—	—	—	1	4	9	10	1	1	—	—	—	63.4±1.1
	Laurentian Cr.	40	—	—	—	—	7	17	8	4	2	2	—	—	63.6±1.3
Total		277	2	2	11	34	57	89	48	16	13	5	—	—	62.9
L. tridentata	Oyster R.	42	—	—	—	—	—	1	5	12	13	10	1	—	65.6±1.2
	Qualicum R.	63	—	—	—	—	—	—	1	9	24	19	9	1	66.5±1.0
	Koksilah R.	61	—	—	—	—	—	1	3	16	21	16	4	—	65.9±1.0
	Chemainus R.	37	—	—	—	—	—	—	—	12	13	11	1	—	66.0±0.9
Total		203	—	—	—	—	—	2	9	49	71	56	15	1	66.1
L. ayresi	Fraser R.	50	—	—	—	—	—	3	10	19	13	5	—	—	65.1

additional sample of 50 ammocoetes (length range 116–142 mm) collected from the Qualicum River July 1978 also exhibited a lightly pigmented caudal ridge. A sample of 25 was preserved for subsequent examination while the remainder were held alive. In October 1978, 48% were nearing the completion of metamorphosis and, based on the dentition pattern, these individuals were positively identified as *L. tridentata*. The remaining ammocoetes metamorphosed the following year and were also *L. tridentata*.

The head pigmentation patterns of *L. tridentata* were variable and not suitable for separating *L. tridentata* and *L. richardsoni*, contrary to views previously reported by Pletcher (1963) and Vladykov and Kott (1976a). In *L. tridentata* the prebranchial blotch was not always present, nor was there always an unpigmented zone above the branchial pores (Fig. 3A). The upper lip and suborbital areas are moderately pigmented and appear grey when preserved (Fig. 3A) or grey-brown in live samples. The degree of pigmentation in the branchial area was difficult to differentiate in live material.

The body proportions of *L. tridentata* ammocoetes expressed as a percent of total length were found to vary according to the total length (Table 1). The size of the prebranchial region relative to total length is larger in smaller individuals, ranging from 13.0 to 6.8% as total length increased from 24 to 145 mm. The proportion of the branchial region to total length is also inversely related to length. The mean proportion of branchial length to total length for ammocoetes in the 20–29 mm length interval was 15.8% compared to 11.0% for ammocoetes in the 140–149 mm range. Decreases in the relative size of the prebranchial and branchial areas were accompanied by increasing trunk and tail proportions. After an initial decrease in the very small length intervals the relative trunk length increased from 49.4 to 51.6% of the total length over a length interval of 65–145 mm. The most noticeable example of allometric growth occurred in the tail region which increased from 18.4 to 30.3% of the total length over the 25–145 mm length intervals. This change occurred mostly among the smaller size classes.

The differences among the number of myomeres (65.6, 65.9, 66.0, 66.5) found in *L. tridentata* ammocoetes (Table 2) from four streams were not significant (*t*-test, $P \geq 0.05$).

The area immediately surrounding the tongue precursor bulb and the associated ridge extension were pigmented (Fig. 4A); the bulb structure was not pigmented.

LAMPETRA RICHARDSONI

Ammocoetes that were not *L. tridentata* had a different tail pigmentation pattern. The taxonomic significance of this second tail pigmentation pattern was studied from a sample of ammocoetes and metamorphosed ammocoetes that were collected from Laurentian Creek (Fig. 1) in November 1977. The tail pattern consisted of intense pigmentation in the area of the caudal ridge, appearing almost black in many cases (Fig. 3C). The extent of pigmentation radiating out to the caudal fin was variable, often giving the caudal fin a mottled appearance in the peripheral region. This pattern was clearly different from that possessed by *L. tridentata* ammocoetes from Qualicum River. The dentition pattern of the metamorphosed ammocoetes in the sample also supported the conclusion that these individuals were not *L. tridentata*. These ammocoetes were tentatively identified as *L. richardsoni*, however, the possibility that this sample might also be a mixture of *L. richardsoni* and *L. ayresi* was not discounted because we had yet to develop criteria for identifying *L. ayresi*. A subsample of 37 ammocoetes (length range 135–213 mm) was held alive until postlarval examination could confirm our identification. By 1980 all ammocoetes in this sample metamorphosed, spawned in the rearing tank, and died. This behavior in addition to the inability of juvenile forms to osmoregulate in salt water confirmed that this second tail pattern was characteristic of *L. richardsoni*.

The head pigmentation of *L. richardsoni* ammocoetes was generally darker than *L. tridentata* when comparing preserved material, however, reliable identification could not be based on head pigmentation. The suborbital and branchial areas are moderately pigmented giving way to light pigment in the ventral region (Fig. 3C). The prebranchial area was moderately to strongly pigmented while the upper lip was

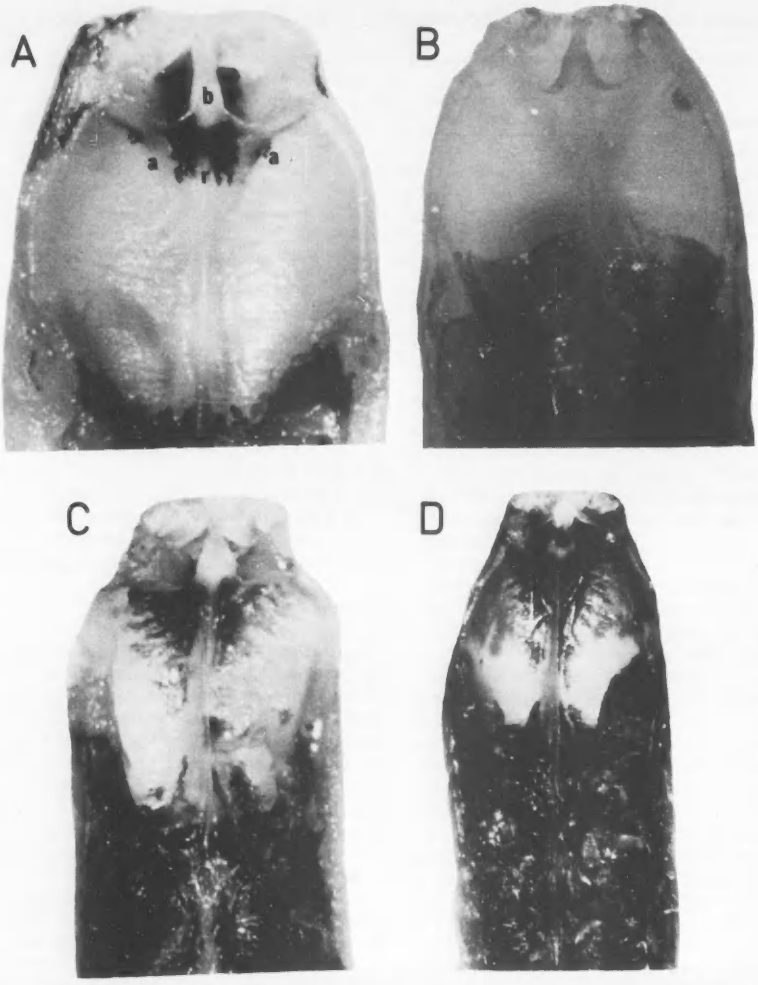

FIG. 4. The pigmentation of the tongue precursor and surrounding area for (A) *L. tridentata*, (B) *L. ayresi*, (C,D) *L. richardsoni*. Figures C, D illustrate the degree of variability which was observed. a, surrounding area; b, tongue precursor bulb; r, tongue precursor ridge.

moderately pigmented.

The changing relative size of body proportions noted among *L. tridentata* ammocoetes was also apparent among *L. richardsoni*. The relative proportion of the prebranchial region expressed in terms of total length decreased from 8.7 to 7.1% as the total length increased from 85 to 185 mm (Table 3). Similarly, the relative size of the branchial region also decreased. Ammocoetes in the 80 to 89 mm interval had a branchial length of 13.8% compared to 11.5% total length for those in the 180–189 mm interval. The relative proportion of the trunk and tail regions increased with increasing total length. Mean trunk lengths for 10 mm intervals ranging from 85 to 185 mm increased from 50.4 to 52.8% while the size of the tail region increased from 27.4 to 28.7% of the total length.

The mean number of myomeres of *L. richardsoni* ammocoetes (Table 2) from five streams (61.9, 63.0, 63.4, 63.6, 64.8) was less than *L. tridentata* but individual counts were variable ranging from 58 to 67. Because of this variation, myomere counts were of little use for identifying ammocoetes.

Pigmentation of the tongue precursor structure and surrounding area in *L. richardsoni* ammocoetes was variable but generally more extensive in the area surrounding the tongue

TABLE 3. Body proportions of *L. richardsoni* ammocoetes from various streams in British Columbia. Values expressed in percent total length ±1 SD.

	Total length (mm)										
	80–89	90–99	100–109	110–119	120–129	130–139	140–149	150–159	160–169	170–179	180–189
Number	3	19	44	59	45	27	22	20	12	2	2
Prebranchial											
Bonsall	—	7.5±0.6	8.3±0.5	7.7±0.7	7.4±0.2	7.5±0.3	7.3±0.2	7.4±0.2	7.1±0.1	—	—
Laurentian	—	—	—	—	8.1	7.5	7.7±0.3	7.2±0.3	7.0±0.4	6.8±0.2	7.1±0.3
Koksilah	—	—	—	—	8.2±0.1	7.7±0.6	7.9±0.5	7.8±0.7	7.1±0.4	—	—
Oyster	8.7±0.2	8.5±0.5	8.4±0.3	8.1±0.6	7.9±0.4	7.7±0.3	7.7	7.6±0.1	—	—	—
Morrison	—	9.3±0.4	8.9±0.3	8.6±0.3	8.4±0.2	8.2±0.3	7.9	—	—	—	—
mean	8.7	8.4	8.5	8.1	7.9	7.7	7.7	7.5	7.1	6.8	7.1
Branchial											
Bonsall	—	13.4±0.2	13.4±0.5	13.3±0.2	12.2±0.4	13.0±0.2	12.3±0.4	12.5±0.4	11.7±0.1	—	—
Laurentian	—	—	—	—	12.3	12.6	11.5±0.5	11.7±1.0	11.5±0.4	11.3±0.1	11.5±0.7
Koksilah	—	—	—	—	12.6±0.3	11.9±0.2	12.1±0.4	12.3±0.8	11.0±0.5	—	—
Oyster	13.8±0.6	13.1±0.5	13.1±0.6	13.1±0.7	12.7±0.6	12.7±0.6	13.4	12.7±0.3	—	—	—
Morrison	—	13.0±0.7	13.2±0.4	12.8±0.5	12.5±0.6	12.6±0.6	11.7	—	—	—	—
mean	13.8	13.2	13.2	13.1	12.5	12.6	12.2	12.3	11.4	11.3	11.5
Trunk											
Bonsall	—	53.4±0.9	51.4±0.8	52.2±0.4	52.2±0.4	52.3±0.8	52.8±0.7	53.0±1.0	53.3±0.1	—	—
Laurentian	—	—	—	—	52.4	51.5	53.4±0.1	54.2±0.8	54.1±1.3	52.6±1.1	52.8±1.3
Koksilah	—	—	—	—	51.2±0.3	51.5±1.3	51.1±1.2	51.9±0.6	53.4±0.6	—	—
Oyster	50.4±1.7	49.6±1.0	50.3±1.9	49.7±1.7	50.4±1.5	51.2±0.8	51.9	50.5±1.1	—	—	—
Morrison	—	49.1±0.7	50.2±1.1	50.6±1.3	51.0±1.3	51.3±1.5	51.4	—	—	—	—
mean	50.4	50.7	50.7	50.8	51.4	51.6	52.1	52.4	53.6	52.6	52.8
Tail											
Bonsall	—	26.4±0.3	26.7±1.7	27.0±1.2	28.1±0.3	27.5±0.5	27.3±0.6	27.3±1.0	27.5±0.5	—	—
Laurentian	—	—	—	—	27.0	28.8	27.2±1.8	27.7±0.6	27.9±1.2	28.9±0.4	28.7±1.4
Koksilah	—	—	—	—	28.5±0.5	28.2±1.5	29.6±1.4	28.5±1.0	29.2±0.7	—	—
Oyster	27.4±0.6	28.3±0.8	28.4±1.3	28.8±1.1	29.1±1.3	28.7±1.2	29.2	28.9±0.9	—	—	—
Morrison	—	28.0±0.6	27.9±1.0	28.1±1.1	28.2±0.6	28.2±0.7	29.1	—	—	—	—
mean	27.4	27.6	27.7	28.0	28.2	28.3	28.5	28.1	28.2	28.9	28.7

TABLE 4. Body proportions of *L. ayresi* ammocoetes from the Fraser River, in British Columbia. Values expressed as percent total length ±1 SD.

	Total length (mm)				
	70–79	80–89	90–99	100–109	110–119
Number	9	18	30	31	11
Prebranchial	7.7±0.3	8.3±0.4	7.5±0.4	7.3±0.3	7.3±0.5
Branchial	13.8±0.6	13.7±0.4	13.2±0.5	13.1±0.4	12.5±0.4
Trunk	52.7±1.1	52.3±0.9	52.1±1.0	52.7±0.8	52.1±1.3
Tail	26.5±1.0	26.8±0.8	27.1±0.7	26.8±0.9	27.6±1.0

precursor in *L. richardsoni* than *L. tridentata* (Fig. 4A, C–D). While in some cases the degree of pigmentation of tongue precursor structures could be used to separate these two species, we recommended it only be used as a secondary characteristic to tail pigment patterns.

Collections of live ammocoetes from the Oyster and Somass rivers (Fig. 1) were identified as either *L. tridentata* or *L. richardsoni* using tail pigmentation patterns. Species from each river were reared separately and in all cases the ammocoetes metamorphosed into the expected species.

LAMPETRA AYRESI[2]

In May 1980, samples of ammocoetes and juvenile lampreys were collected from the Fraser River. The juveniles were identified as *L. ayresi* on the basis of sharp cornified teeth, silver lateral body pigmentation, and the immature condition of the gonads. These characters were not found in samples of juvenile *L. richardsoni* at this time of year.

The tail pigmentation of ammocoetes in the Fraser River sample had less pigmentation than *L. richardsoni* and while many had a caudal ridge that was uniformly darkly pigmented, some had a light caudal ridge similar to *L. tridentata* (Fig. 3D). We consider that the tail pigmentation pattern should be accepted as variable but in general to be intermediate between *L. richardsoni* and *L. tridentata*. The pigmentation in the head region was reduced and very different from the other species, giving these ammocoetes a lighter appearance than either *L. richardsoni* or *L. tridentata* (Fig. 3D). The suborbital, prebranchial and branchial areas were unpigmented while the area anterior to the eye spot contained the most pigment. The most startling feature of the head pigmentation was the thin dark streak immediately anterior to the eye spot and the dark line that extends posteriorly from the eye spot to a position above the first branchial pore. The other species have this dark line posterior to the eye spot but its prominence is greatly accentuated in *L. ayresi* because of the absence of surrounding pigmentation. This pattern of pigmentation was consistent with a previously published description of *L. ayresi* ammocoetes (Vladykov and Follett 1958), therefore these ammocoetes were tentatively identified as *L. ayresi*. A subsample of 180 ammocoetes (length range 37–122 mm) was held alive and fed as previously described. In January 1981, five postlarval individuals were examined and identified as *L. ayresi*. Unlike juvenile and adult *L. richardsoni* these lampreys had strong sharp dentition.Three of the five juveniles were able to osmoregulate in salt water. The two that died during the transfer into salt water were extremely small and appeared emaciated. The dentition of these lampreys and their ability to survive in salt water confirmed that they were *L. ayresi*.

Changes in the relative proportions of the various body regions with respect to total length were also evident among *L. ayresi*. The relative sizes of the prebranchial and branchial regions were inversely related to total length. Mean length of the prebranchial region for 10 mm length intervals from 75 to 115 mm decreased from 7.7 to 7.3% (Table 4). Similarly, the proportion of relative branchial length to total length decreased from 13.8 to 12.5%. Little change occurred in the size of the trunk region which varied from 52.1 to 52.7% of the total length. The proportion of tail length to total length increased from 26.5% in the 70–79 mm length interval to 27.7% in the 110–119 mm length interval. Myomeres from 50 *L. ayresi* ammocoetes ranged from 63 to 67 with a mean value of 65.1 (Table 2).

As noted by Vladykov and Follett (1958), the tongue precursor in *L. ayresi* ammocoetes had a bulb, ridge, and surrounding area that were completely devoid of pigment (Fig. 4B). This unpigmented condition clearly separates *L. ayresi* from the other two species examined in this study.

Unfortunately it was not possible to maintain the reared *L. ayresi* and *L. richardsoni* beyond 2 yr. The intention was to compare pigmentation patterns annually to determine if pigmentation pattern could be used to separate these species during early development. It was possible to show that the head pigmentation pattern of *L. ayresi* and *L. richardsoni* ammocoetes was established during the first year. The pigmentation in the tail region that was characteristic of larger ammocoetes was not prominent in the first year for either species or in the second year for *L. ayresi*.

Discussion

Some of the published taxonomic criteria for the three species of lamprey ammocoetes examined during this study were found to be inadequate for species identification, particularly when samples were alive. The head pigmentation pattern we observed for *L. tridentata* differed from that described by Vladykov and Kott (1976a). They described an unpigmented band above the branchial pores as being a characteristic which distinguished *L. tridentata* from other closely related species. The *L. tridentata* ammocoetes we examined

[2]The 4-cm juvenile river lamprey recorded in Beamish (1980, p. 1908, Table 1) is unavailable for confirmation and is probably an error; however, we do have a specimen measuring 69 mm.

TABLE 5. A key to ammocoetes in coastal streams in British Columbia. Arrows indicate key features.

1. Tail lightly pigmented in the caudal ridge area; body and head extensively pigmented 3

2. Tail darkly pigmented in the caudal ridge area; or tail lightly pigmented and body and head with reduced pigmentation 4

3. Reduced pigmentation around tongue precursor structure; pigmentation in the suborbital area reduced; may have unpigmented spot above first branchial pore ..... *Lampetra tridentata*[a]

Lampetra macrostoma

4. Area surrounding the tongue precursor structure heavily pigmented; extensive pigmentation in the branchial, prebranchial, and suborbital area..... ..... *Lampetra richardsoni*

5. Reduced pigmentation in the branchial, prebranchial, and suborbital area; prominent line behind eye; area surrounding tongue precursor structure unpigmented ..... *Lampetra ayresi*

[a]*Lampetra* (*Entosphenus*) *tridentata* is the common representative, however, the ammocoetes from Mesachie Lake and Lake Cowichan (Fig. 1) could be *Lampetra macrostoma* or *Lampetra tridentata*. Studies to date indicate that ammocoetes found in these two lakes have been *Lampetra macrostoma*.

clearly showed that in many cases pigment in the branchial region extended down to the branchial pores. Pletcher (1963) described a broad unpigmented blotch anterior and dorsal to the first branchial pore as a characteristic distinguishing *L. tridentata* from other species. Our study showed that this character was variable and should therefore not be used as a primary identifying character.

The heavy pigmentation we found in the suborbital and prebranchial region of *L. richardsoni* ammocoetes is in agreement with the findings of Pletcher (1963) and Vladykov and Follett (1965). However, identification of this species on the basis of this pigmentation was shown not to be possible because there was no consistent difference between *L. tridentata* and *L. richardsoni*.

The pigmentation pattern in the tail region is the only acceptable external character distinguishing *L. tridentata* from *L. richardsoni* ammocoetes and is useful whether the material is alive or preserved. There is no difficulty in interpreting the distinctive light caudal ridge, characteristic of *L. tridentata* ammocoetes. The pigmentation of the tails of *L. ayresi* and *L. richardsoni* can be similar and other characters are required for separating these species.

The results of this study validated the earlier description by Vladykov and Follett (1958) that stated reduced head pigmentation was an identifying criterion for *L. ayresi* ammocoetes. The reduced pigmentation in all areas of the head, except the dorsal surface and around the eye spot, was easily distinguishable from the predominantly heavy pigmentation on *L. richardsoni* ammocoetes.

Vladykov and Follett (1958) described the tail pigmentation patterns for *L. ayresi* and *L. fluviatilis* and claimed that the reduced pigmentation in the tail of *L. fluviatilis* was a

suitable character for separating these two species. The separation of these two species was not reexamined in this study, however, the illustration of the tail pigmentation pattern provided by Vladykov and Follett (1958) for *L. ayresi* is an extreme condition, identical to *L. tridentata*, and not the common pattern in our samples.

If preserved material is being examined it is possible to look at additional taxonomic characters that are useful for identification. The pigmentation of the tongue precursor was useful for separating *L. ayresi* from *L. richardsoni* and *L. tridentata*; *L. ayresi* ammocoetes are distinguishable by the absence of pigmentation in this region. The reduced pigmentation around the tongue precursor structure in *L. tridentata* ammocoetes compared to *L. richardsoni* ammocoetes was consistent and useful for separating these species if there is doubt about tail pigmentation.

The number of myomeres and body proportions of ammocoetes were not useful characters for separating species because of the variation in counts and measurements. For example, the mean myomere values of *L. richardsoni* ranged from 61.9 for Oyster River ammocoetes to 64.8 for Bonsall Creek ammocoetes (Table 2). This is also inconsistent with the work of Vladykov and Follett (1965). They examined 121 ammocoetes from British Columbia and Washington and determined a mean of 60.7 myomeres, much lower than in any of the stream populations we examined. Our values were in closer agreement to the mean of 62.3 myomeres determined by Pletcher (1963) for ammocoetes collected in British Columbia.

Variation in the relative body proportions of ammocoetes of *L. richardsoni* occurred among samples from various rivers. This, in addition to the problem of allometric growth among lampreys, limits the usefulness of body proportions as identifying criteria. Meaningful comparisons of body proportions can only be made between similar sized intervals, and it is unknown at this time if age as well as size is important. Even when similar sized individuals are compared the measurements overlap significantly for the different species.

Interestingly intraspecific variation in the number of myomeres and body proportions was not as apparent among *L. tridentata* ammocoetes as they were for *L. richardsoni*. The difference between mean myomere counts of *L. tridentata* ammocoetes from the four rivers examined was not significantly different (t-test, $P \geq 0.05$). The pooled overall mean of 66.1 was in agreement with the findings of Pletcher (1963) yet lower than 67.6 and 68.7 reported by Vladykov and Kott (1976a) and Vladykov and Kott (1976b), respectively. It is possible that regional differences exist in *L. richardsoni* populations as a result of the isolated distribution of these nonparasitic freshwater species. This is in contrast to *L. tridentata* which may interbreed as a consequence of an absence or a breakdown in homing during its spawning migration from the marine environment. Meristic variation among *L. ayresi* ammocoetes could not be examined because only one source of ammocoetes was available.

In another study, *L. macrostoma* ammocoetes could not be distinguished from *L. tridentata* ammocoetes (Beamish 1982). Ammocoetes were reared through metamorphosis and confirmed to be *L. macrostoma*. The pigmentation was much darker and the ammocoetes grew to larger sizes, however, the pigmentation patterns of these ammocoetes were not sufficiently different to distinguish them from *L. tridentata* (Fig. 3B). Because the distribution of *L. macrostoma* appears restricted to a few freshwater lakes we suggest that until suitable characters can be found, ammocoetes from these watersheds should be considered to be either *L. macrostoma* or *L. tridentata*.

Vladykov and Kott (1976a) also found that the head pigmentation pattern was similar among ammocoetes of species that were considered to be derivatives of *L. tridentata*. In their report they describe a broad unpigmented band above the branchial pores in *L. tridentata* as a suitable character for separating *L. tridentata* from three related species but were unable to separate the three related species. Our rearing studies showed that this character is variable and therefore should not be used to separate *L. tridentata* ammocoetes or its derivatives.

A summary of the criteria for the identification of live and preserved ammocoetes from coastal streams of British Columbia is presented in a key in Table 5.

The ability to identify lamprey ammocoetes is a key step in attempting assessments of the relative biomass of the various species. Knowledge of the relative biomass of the major parasitic species is necessary before the impact of lampreys on commercial fisheries can be estimated.

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Stock-Recruitment Relationship for Atlantic Salmon (*Salmo salar*) in Newfoundland Rivers

E. M. P. CHADWICK

Fisheries Research Branch, Department of Fisheries and Oceans, P.O.Box 5667, St. John's, Nfld. A1C 5X1

CHADWICK, E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. 39: 1496 – 1501.

A stock-recruitment relationship was developed for Atlantic salmon (*Salmo salar*) in Western Arm Brook, a small Newfoundland river. Supportive evidence was also found on Indian and Little Codroy, two other Newfoundland rivers. On Western Arm Brook, year-class strength of smolts was correlated ($P < 0.01$) with egg deposition. On Little Codroy River, smolt year-class strength was correlated ($P < 0.01$) with potential egg deposition of adults counted as kelt. On Indian River egg to fry survival was correlated ($P < 0.01$) with winter temperature and discharge. On the basis of these findings, the current recommended egg deposition of 2.4 eggs$\cdot$m^{-2} of parr-rearing habitat was considered inadequate for Newfoundland rivers.

Key words: stock-recruitment, Atlantic salmon

Chadwick, E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. 39: 1496 – 1501.

Nous avons établi une relation stock-recrutement pour le saumon atlantique (*Salmo salar*) dans le ruisseau Western Arm, un petit cours d'eau de Terre-Neuve. Cette relation est en outre appuyée par des données recueillies dans les rivières Indian et Little Codroy, également à Terre-Neuve. Dans le ruisseau Western Arm, il y a corrélation ($P < 0{,}01$) entre les effectifs de classe d'âge des smolts et le nombre d'oeufs déposés. Dans la rivière Little Codroy, les effectifs de classe d'âge des smolts sont en corrélation ($P < 0{,}01$) avec le nombre potentiel d'oeufs déposés par des adultes dénombrés comme charognards. Dans la rivière Indian, la survie de l'oeuf à l'alevin est en corrélation ($P < 0{,}01$) avec la température et le débit. D'après ces résultats, on est d'avis que le nombre d'oeufs déposés présentement recommandé de 2,4 oeufs$\cdot$m^{-2} d'habitat d'élevage jusqu'au stade tacon est inadéquat pour les rivières de Terre-Neuve.

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AN important objective in management of Atlantic salmon (*Salmo salar*) is to develop stock-recruitment relationships. Relationships between spawners (stock) and their offspring (recruits) are necessary to manage both discrete and mixed-stock fisheries. Currently, in Newfoundland and Labrador most salmon are exploited in coastal, mixed-stock fisheries. There is considerable criticism of this type of fishery because it is difficult to manage for individual stocks without having an impact on others. However, to change the fisheries towards river harvest, biologists must calculate optimal spawning requirements for individual stocks. Stock-recruitment relationships are also necessary to predict abundance of stocks well before harvest. Predictions of stock size made several years in advance allow fisheries to be properly regulated with a minimum of economic hardship. Finally, enhancement of stocks requires stock-recruitment relationships to measure the costs and benefits of enhancement against natural propagation.

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Earlier attempts to obtain predictive stock-recruitment relationships for Atlantic salmon were based on the Ricker model (Ricker 1954). Harvest statistics were assumed to reflect stock and recruitment of individual populations; biological characteristics such as smolt age, sea age, and sex ratio were usually assumed to remain constant; changes in environmental conditions were also assumed to have negligible impact. Not one of these assumptions was entirely valid because of unknown harvest of individual stocks in mixed-stock fisheries, large annual variations in biological characteristics (Chadwick 1981), and possibly environmental influences on year-class strength, such as changes in water temperature (Lishev and Rimsh 1961; Hunt 1969; Chadwick 1980; Lind 1980) and discharge (Azbelev 1960; Havey 1974; Havey and Davis 1970). Consequently, attempts to develop stock-recruitment curves on Ellidaar River (Mundy et al. 1978), Foyle River (Elson and Tuomi 1975), Miramichi River (G. Turner, Fisheries and Oceans, Halifax, N.S., personal communication) and rivers of Labrador (Dempson 1980), insular Newfoundland (E. M. P. Chadwick, unpublished

data) and St. Georges Bay (B. Dempson, Fisheries and Oceans, St. John's, Nfld., personal communication) have been only partly successful.

A simple way to determine a stock-recruitment relationship for Atlantic salmon is to count spawning adults (stock) and smolts (recruitment) directly in a river. Smolts are a good index of recruitment for two reasons: first, they are the last measure of abundance of Atlantic salmon, before harvest in the fisheries; and second, the abundance of smolts is correlated with the abundance of 1SW salmon in the following year (Chadwick et al. 1978). (1SW salmon spend 1 yr at sea before first spawning (Allan and Ritter 1977).) However, this type of information is not readily available for natural populations. The longest, suitable time series is Western Arm Brook (WAB), Newfoundland (Chadwick 1981). This time series is suitable because the counts of smolts and adults are complete, the watershed is free of human influence, and the population has been handled to obtain only small scientific samples. Although fairly short, covering only 11 yr and six generations, this time series is sufficient for an examination of evidence of a stock-recruitment relationship. Similar data from two other Newfoundland rivers, Little Codroy and Indian, are also available for comparison. A supplementary objective of my study was to focus more attention on experimental rivers as a basis for rational salmon fisheries management.

Methods

Migrations of Atlantic salmon smolts and adults have been counted on Western Arm Brook (Fig. 1) for 11 yr (1971–81). Details on the size and biological characteristics of the migrations are presented elsewhere (see Chadwick 1980, 1981; Chadwick et al. 1978). The stock-recruitment relationship was calculated using natural logarithmic transformations on both number of eggs deposited and the sizes of year-classes of smolts which resulted.

The time series on WAB was enough to follow five complete year-classes from egg deposition to their recruitment as smolts. It was possible to estimate a sixth year-class by assuming that the size of the 5+ cohort was equal to the mean of other years. However, only five year-classes were included in the regression; the 1972 year-class was considered to be an outlier and it was not included in the analysis.

Evidence to suggest that the 1972 year-class was anomalous relative to other year-classes was obtained by comparing egg to smolt mortality rates to environmental information during the first year of life history. The first year of life history is usually considered to be most sensitive to environmental influence. Two environmental factors were used, winter air temperature and water discharge. Winter air temperature was taken from the sum of mean temperatures for December, January, February, and March at St. Anthony. Temperature at this location was assumed to be comparable to WAB, although it is 90 km northwest of the river mouth. Temperatures taken from Monthly Record (Anon. 1971-78) in °F were converted to °C. Water discharge was taken from St. Genevieve River (Fig. 1), which is adjacent to WAB (Anon. 1977). Both rivers flow over similar topography and they should be fairly similar in hydrographic characteristics.

FIG. 1. Insular Newfoundland and southern Labrador showing rivers and place names mentioned in text.

A ratio was used to express the difference between water discharge at the time of spawning and during the coldest winter month. The ratio was calculated from the sum of mean monthly discharges in January, February, and March as a proportion of the sum of mean monthly discharges in September, October, and November in the previous year. Presumably, egg or fry survival would be impaired in cold years with a low water discharge (Power 1969; Taylor 1973).

Spawning stock or egg deposition on WAB was calculated from the 1971–80 adult migrations. Fecundity (F) was estimated each year from mean fork length (L) using $\text{Log}_{10}F = 2.3345, \text{Log}_{10}L - 0.582$ (Pope et al. 1961). Several assumptions were required. First, the sex ratio was assumed to be 74% females in all years. Unfortunately, sex ratios were not reliable in some years because of small sample sizes. The 74% value was based on external sex determinations of 780 adult salmon of which, 574 fish were female. Secondly, mean fork length was calculated for both sexes combined as there was negligible difference between the size of males and females (E. M. P. Chadwick, unpublished data). The third assumption was that there was a constant, but negligible, mortality of spawning adults after they had been counted at the fish trap.

Stock and recruitment were also examined on Little Codroy River (Murray 1968a, b and E. M. P. Chadwick, unpublished data). It was the only other river in Atlantic Canada with a 10-yr continuous time series of relatively complete counts of

TABLE 1. Prediction of year-classes of smolt from egg deposition on Western Arm Brook. Predicted values are in parentheses.

Year-class	X Thousands of eggs	Y Year-class as smolts	95% confidence limits
1973	428	6074	
1974	787	13316	
1975	667	11864	
1976	827	12646	
1977	870	16932	
1978	737	(12456)	(10883–14257)
1979	572	(8991)	(7631–10594)
1980	3024	(77188)	(36098–165049)

$\ln Y = 1.29 \ln X - 8.014$
$r = 0.971 \quad P < 0.01$

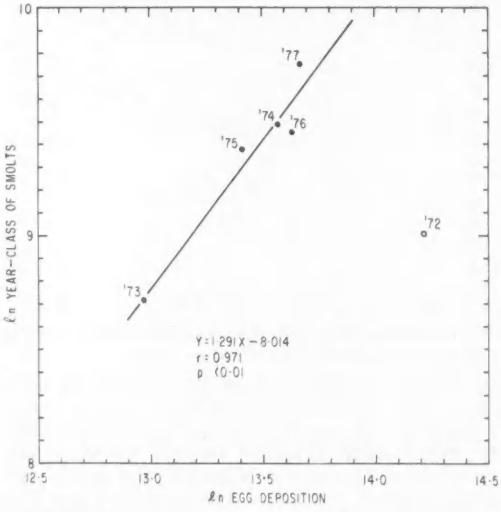

FIG. 2. Relationship between egg deposition and year-class strength as smolts on Western Arm Brook. Year-classes are indicated.

smolts and kelts. Counts of escaping adults were not complete during the first several years of operation due to a run of large salmon in late October after the counting fence had been removed (Anon. 1957). Thus kelts were used as an index of the numbers of fish spawning during the previous year and to calculate egg deposition (Chadwick 1980); recruitment was calculated from their progeny as year-classes of smolts. The number of kelt was increased by 40% to account for fish which did not survive spawning. This value was obtained from WAB where mean overwinter survival from spawning adults to kelts was 60% (Chadwick 1981). A simple regression was calculated using a natural logarithmic transformation on both variables.

A multiple linear regression was used to test the influence of winter temperature and water discharge on egg to fry survival at the spawning channel on Indian River. Indian River was the only river in Newfoundland where this type of information was available. Mean monthly air temperatures were available for Springdale, near the mouth of Indian River from Monthly Record (1963–72). The temperature of the month with the lowest mean within each year was used as the X variable. The mean water discharge during the coldest month was subtracted from the month of greatest discharge prior to freeze up, either November or December. This value was used as the Y variable. Mean monthly water discharges were available for Indian River in Historical Streamflow Summary (Anon. 1977). Water flows in the spawning channel were not regulated during winter months. Egg to fry survival rates were available on Indian River from 1963 to 1972 (Anon. 1978). They were treated with an arc sine transformation and used as the Z variable. A number of independent variables were also examined, including those that were used on WAB (i.e. winter temperature and discharge ratio), but the only significant relationship to explain egg to fry survival was found using the variables described above.

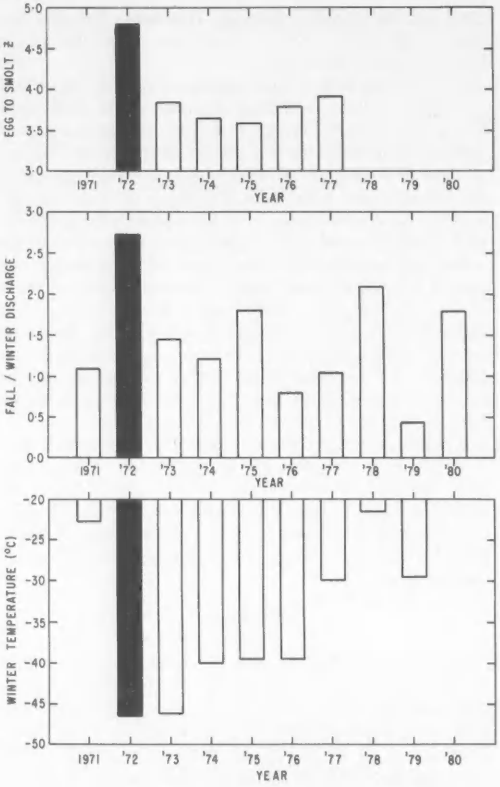

FIG. 3. Egg to smolt survival on Western Arm Brook; discharge on St. Genevieve River; and, winter air temperature in St. Anthony.

Results

Year-class strengths of smolts on WAB were correlated

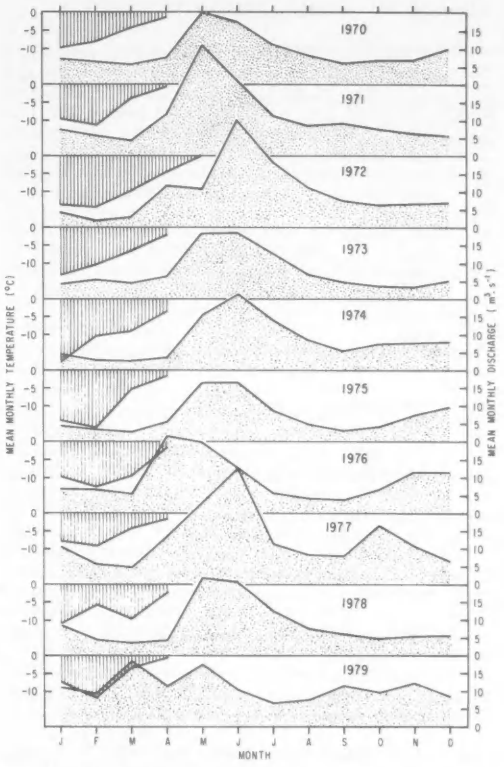

FIG. 4. Mean monthly discharge on St. Genevieve River (1970–79) and mean monthly air temperature (January–May) for St. Anthony.

with egg deposition (Table 1, Fig. 2). The regression was significant ($P < 0.01$). The size of the 1978–80 year-classes was calculated along with 95% confidence limits (Table 1). The 1980 year-class promises to be 77 188 smolts, which is more than six times current smolt production.

The 1972 year-class was omitted from the regression because its egg to smolt mortality rate was so much greater than the other five year-classes. It appeared that this greater mortality rate was the result of both low winter discharge and cold winter temperatures (Fig. 3 and 4).

Smolt year-class strength on Little Codroy River was significantly correlated ($P < 0.01$) with the potential egg deposition of kelts (Table 2). This indicated that kelts were either a good index of spawners, or the same environmental conditions affected both hatching success and overwinter survival of kelts.

Egg to fry survival on Indian River was significantly correlated ($P < 0.01$) with winter temperature and discharge (Table 3). Detailed examination of the data revealed there was low survival during cold winters with low water discharge, especially when there was high water discharge during spawnings. Thus, fish which spawned under conditions of above-average discharge had redds which were possibly more vulnerable to exposure and freezing.

TABLE 2. Regression of smolt year-class strength (Y) and egg deposition (X) on Little Codroy River. Egg deposition was calculated using kelt as an index of spawners (Chadwick 1980).

	X	Y
Year-class	Thousands of eggs	Smolt year-class size
1954	1360	12 490
1955	455	8 911
1956	542	11 533
1957	370	8 945
1958	82	5 354
1959	352	8 164
1960	185	7 799

$\ln Y = 0.302 \ln X - 5.223$
$r = 0.954 \quad P < 0.01 \quad df = 5$

Discussion

The stock-recruitment relationships on WAB (Table 1, Fig. 2) and Little Codroy River (Table 2) were the first developed for Atlantic salmon. The relationships are based on only a few observations but they are important because they indicate that smolt production can be predicted from egg deposition and that it is possible to calculate optimal spawning requirements. The 1980 year-class on WAB (Table 1) will be especially valuable in this latter aspect due to the very large egg deposition. It is also noteworthy that the two relationships were so similar. Both the adjusted egg to smolt survival rates and their annual variation were nearly equal on both rivers (Table 4). This indicates that freshwater survival of salmon is similar on very different watersheds.

There are good reasons for omitting the 1972 year-class from the time series on WAB. The egg to smolt mortality rate of this year-class was 50% greater than the other five year-classes (Fig. 3). Rather than omit the observation outright, I attempted to find a biological mechanism which would explain why it was different. The poor survival rates of the 1972 year-class appeared to be caused by a combination of cold winter temperatures and low winter discharge (Fig. 3 and 4). The poor survival could have been egg mortality due to freezing of redds. A similar mechanism has been described by Power (1969) and Taylor (1973). This was corroborated by the data on Indian River, where egg to fry survival was correlated with winter temperature and discharge (Table 3). The slightly different method for calculating the independent variables on Indian River could reflect the different hydrological characteristics between it and WAB. Thus, it seemed reasonable to omit the 1972 year-class from the stock-recruitment relationship.

It is possible that optimal spawning requirements are much higher than previous estimates. My results are not adequate to determine a yield curve; a longer time series would be required. A comparison with current estimates of spawning requirements, however, is instructive. Spawning requirements for Atlantic salmon in Canadian rivers have been

TABLE 3. Indian River spawning channel: relationship between winter temperature, change in water level and egg to fry survival.

	X	Y	Z
Year	Lowest winter mean mo. temp. (°C)	Difference between Nov. and lowest winter mean mo. discharge ($L \cdot s^{-1}$)	Egg to fry survival arc sin $\sqrt{P}$[a]
1963–64	−9.1	3824	32.6
1964–65	−8.1	4306	39.2
1965–66	−6.4	1360	53.7
1966–67	−10.9	1133	38.1
1967–68	−7.9	5212	35.1
1968–69	−4.3	2351	39.2
1969–70	−9.4	4334	22.0
1970–71	−9.1	453	54.9
1971–72	−12.0	4561	20.3

$Z = 68.07 + 1.89X - 0.005Y$
$r = 0.844$ df = 6 $P < 0.01$

[a]P = egg to fry survival as a proportion.

TABLE 4. Summary of mean smolt age and egg to smolt survival rates on three Atlantic salmon rivers.

Parameter	Pollett River	Little Codroy River	Western Arm Brook
Smolt age (yr)	2.1	2.6	3.9
% survival (egg to smolt)	1.1	2.9	1.7[a]
% survival adjusted to smolt age 2.1 yr	1.1	3.6	3.2
Coefficient of variation in annual smolt production	64%	27%	30%

[a]excluding 1972 year-class.

estimated from experiments on Pollett River, N.B. (Elson 1957, 1975). Stock size was estimated from natural egg deposition and planted hatchery fry and recruits were measured as their smolt progeny. Elson (1975) concluded that an egg deposition of 2.4 eggs $\cdot m^{-2}$ of suitable rearing habitat (Fig. 2) gave "optimal" smolt production, and he also recommended levels for fry, small parr, and large parr densities. These values are widely used throughout Atlantic Canada (Anon. 1978), but I suggest they should be used with caution: salmon habitat is difficult to measure and may not be comparable between different rivers; Pollett River was manipulated and may not represent natural systems; and, an egg deposition of 2.4 eggs $\cdot m^{-2}$ may only be an arbitrary figure.

Salmon habitat is quite variable. In Newfoundland rivers, where there are no cyprinids or percids, Atlantic salmon are abundant in lentic as well as in riffle-pool habitats. For example, in WAB, about 70% of smolts are produced in 1960 ha of lakes and 44 ha of slow-flowing steadies (E. M. P. Chadwick, unpublished data), and the conversion of egg deposition and smolt production to the 9.9 ha of standard smolt rearing habitat leads to inflated values (Chadwick 1981) which are then somewhat meaningless.

Pollett River may not be comparable to other rivers because fish-eating birds namely, mergansers and kingfishers, were actively removed before the experiment. The egg to smolt survival rates and annual variation in smolt production were quite different from Little Codroy River and WAB. This was most clearly seen when the egg to smolt survival rates on all three rivers were adjusted to the same smolt age of 2.1 yr. The survival rate on Pollett River was considerably lower (Table 4). This was somewhat surprising as the removal of major predators should have increased the survival. Possibly, other factors were involved or predation by birds is not the primary cause of mortality in Atlantic salmon. On Pollett River, the coefficient of variation in annual smolt production was twice that found on Little Codroy River and WAB (Table 4); the values on the latter two rivers were almost equal. This greater variation on Pollett River could have been a consequence of the predator control and as such the results may not apply to other rivers.

There seems to be little evidence to support the recommended egg deposition of 2.4 eggs $\cdot m^{-2}$. Elson (1975) indicated optimal egg deposition was the asymptote of a relationship between eggs and smolts on the Pollett River. However, a linear fit ($r = 0.83$) had smaller residuals than Elson's (1975) curvilinear relationship ($r = 0.81$) suggesting that the asymptote had not been reached. Therefore, I emphasize the critical need for more research on experimental rivers. Possibly optimal egg deposition could be considerably higher on many salmon rivers.

Acknowledgments

This paper is based largely on information collected by many dedicated biologists and technicians in our Branch (Freshwater and Anadromous Fisheries Management Program) before my arrival in 1976. In this regard, I acknowledge the careful work of Al Murray and Jerry Pratt. I am particularly grateful for the support and constructive criticisms of Rex Porter. I also thank Scott Akenhead, Brian Dempson, John Pippy, Rex Porter, J. Pella, and another anonymous reviewer for reviewing the manuscript.

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Competitive Interactions Between Benthic Stream Fishes, Riffle Sculpin, *Cottus gulosus*, and Speckled Dace, *Rhinichthys osculus*

DONALD M. BALTZ, PETER B. MOYLE, AND NED J. KNIGHT

Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

BALTZ, D. M., P. B. MOYLE, AND N. J. KNIGHT. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. Can. J. Fish. Aquat. Sci. 39: 1502–1511.

Two morphologically dissimilar stream fishes occupied the same microhabitat in different riffles of Deer Creek, Tehama County, California. In a 12.5 km reach of the creek, speckled dace (*Rhinichthys osculus*) dominated riffles at the lower end while riffle sculpin (*Cottus gulosus*) dominated the riffles at the upper end, where dace were confined to slower water. Between these sets of riffles, relative abundances of the two species were negatively correlated. Routine metabolic rates of sculpin increased rapidly with temperature and indicated that sculpins were unable to tolerate temperatures in the low elevation riffles in the summer. Dace swimming performance appeared to be adequate at low temperatures to permit them to occupy the sculpin-dominated riffles. However, stream tank experiments indicated that at low temperatures sculpin were able to displace dace from cover in high velocity water. Our analysis thus demonstrated that competitive interactions between dace and sculpin for preferred microhabitat were mediated by temperature.

Key words: competition, critical swimming velocity, experimental stream, microhabitat utilization, routine metabolism

BALTZ, D. M., P. B. MOYLE, AND N. J. KNIGHT. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. Can. J. Fish. Aquat. Sci. 39: 1502–1511.

Deux poissons fluviatiles morphologiquement différents occupent le même micro-habitat de différents maigres du ruisseau Deer, comté de Tehama, en Californie. Dans un segment de 12,5 km du ruisseau, le naseux moucheté domine les maigres à l'extrémité d'aval, alors que le chabot de maigre est dominant à l'extrémité d'amont, endroit où le naseux est confiné à l'eau plus lente. Il y a corrélation négative entre l'abondance relative des deux espèces dans ces deux séries de maigres. Les taux métaboliques de routine du chabot augmentent rapidement avec la température, signe que l'espèce ne peut tolérer les températures estivales des maigres situés à faible élévation. La performance natatoire des naseux semble adéquate aux basses températures pour qu'ils puissent occuper les maigres dominés par les chabots. Cependant, des expériences en bassins dans le ruisseau indiquent qu'à de basses températures, les chabots peuvent déplacer les naseux de leur abri en eau rapide. Notre analyse démontre donc que les interactions compétitives entre les naseux et les chabots quant au micro-habitat préféré sont reliées à la température.

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THE role of interspecific competition in determining the distribution and abundance of temperate stream fishes is poorly understood. Competition between salmonids and nongame fishes is frequently cited as a major factor limiting salmonid populations, but the actual evidence is weak (Moyle 1977; Holey et al. 1979; Brown and Moyle 1981). The only studies that clearly demonstrate that stream fishes can be limited by interspecific competition have dealt with pairs of similar species, usually members of the same family (e.g. Caldwalladder 1975; Fausch and White 1981; Schoenherr 1981). Competition between morphologically dissimilar species is generally considered to be unlikely because morphological differences in co-occurring species are presumed to reflect coevolution which minimizes competition (Gatz 1979; Connell 1980). We have found in this study, however, that competition for space between two morphologically dissimilar and presumably coevolved stream fishes can occur. The two species are the riffle sculpin (Cottidae: *Cottus gulosus*) and the speckled dace (Cyprinidae: *Rhinichthys osculus*). The sculpin is a small ambush predator characterized by its large flattened head,

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large mouth, rounded tail, and wide pectoral fins. The dace is a small, active bottom browser with a streamlined body, forked tail, and small, subterminal mouth.

The study began when we noticed that in a 12.5 km long section of Deer Creek (Tehama County, California) riffle sculpins dominated the riffles at the upper end, while speckled dace dominated the riffles at the lower end. This section marks the emergence of Deer Creek from its mountain canyon to the floor of the Sacramento Valley. The major physical difference noted between the riffles at the upper and lower ends was that summer water temperatures were considerably higher and more variable in the lower riffles. We also noticed that although the sculpins were very rare in the lower end of the valley reach, speckled dace were abundant at the upper end, but only in the quiet water at the edges of riffles or in nearby runs. Similar segregation of dace and sculpins was also observed at another study site in the canyon, 30 km upstream. It appeared from these observations that riffles were the preferred habitat of both species but that dace were able to occupy the riffles only when sculpins were excluded by high temperatures. To test this idea we first conducted field studies to determine (1) the relative abundances of the two species in riffles throughout the emergent section of stream, (2) the microhabitats of both species in areas where dace and sculpin occurred together, as well as where dace occurred by themselves, and (3) dietary overlap in the two species. Because these studies indicated that some sort of interaction was taking place between the two species, we next brought them into the laboratory to test the relative importance of physiological responses and behavioral interactions in determining microhabitat utilization. Accordingly we (1) measured the routine metabolic rates of both species at various temperatures, (2) examined the swimming performance of dace at various temperatures, and (3) observed behavioral interactions between the species in an artificial stream in which shelter was a limited resource.

Materials and Methods

Distribution and Abundance

Deer Creek is a moderate sized stream (summer flows 3–6 $m^3 \cdot s^{-1}$) located in the northern Sacramento Valley (WSP 1950). It is one of the least disturbed major streams in the Sierra Nevada foothills and contains a large complement of the native stream fishes. The sculpin and dace transition area is located in the valley reach (elevation 150 m) and is divided into three zones: the upper sculpin-dominated zone, the lower dace-dominated zone, and a middle sympatric zone. A site above the transition area was located in the canyon at an elevation of 460 m.

To test the hypothesis that dominance of dace or sculpin in a riffle was not related to riffle sequence and consequently temperature, we sampled 12 riffles (in the sculpin–dace transition area) during August 11–13, 1980. Sampling was by means of a Smith–Root Type V Electrofisher. A unit of effort was considered to be a three second shocking interval in front of a 0.5 m wide dip net (i.e. 0.25 m^2). The following year, a Ryan Model J recording thermograph was placed at both ends of the reach between May 28 and October 8, 1981 to document more thoroughly the temperature differences between the upper and lower ends of the valley reach.

Microhabitats of the fish were determined to test the hypotheses that (1) sculpins and dace do not differ in their microhabitats when they occur together and (2) dace do not shift their microhabitats in the presence of sculpins. The following data were recorded: (1) water velocity at the place the fish was located (i.e. focal point velocity) (2) mean water column velocity, (3) distance from the bottom where the fish was located (i.e. focal point depth), (4) maximum depth, (5) substrate type below fish, (6) number of individuals, and (7) estimated length of the fish. Velocity was measured with a Marsh–McBirney electronic flow meter mounted on a top-setting wading rod. When the water depth exceeded 0.75 m or the water column was obstructed, mean water column velocity was calculated from velocities taken at proportional depths of 0.2, 0.6, and 0.8 of the maximum depth. Otherwise the velocity at a proportional depth of 0.6 was used (Bovee and Milhous 1978). The substrate composition was estimated from the modified Wentworth particle size scale (Bovee and Cochnauer 1977). Maximum depth and focal point depth were read directly on the wading rod. Focal point depths and focal point velocities were reported only for underwater observations. Our data on maximum depth and mean water column velocity were transformed ($\log_{10} x + 1$) to satisfy the normality and equal variance assumptions of ANOVA. Statistical tests reported for these variables are for transformed data, but the means and distributions reported are not scaled. For analysis, the measurements were stratified by reach and size class. Size classes were comparable and mean lengths of dace (46.7 mm SL, $n = 314$) and sculpins (45.6 mm SL, $n = 468$) were similar, as were the length frequency distributions (available from authors). All dace below 30 mm SL were treated separately as juveniles, as were all sculpins below 40 mm SL (Moyle 1976). Overlap in microhabitat utilization was calculated between species and size classes by Schoener's (1970) formula.

Dietary Overlap

We examined the stomach contents of both species to test the hypothesis that they did not differ in their diets and also to see if they both fed mainly on riffle organisms. Prey were identified to the lowest taxa possible, counted, and weighed. Fish for dietary analysis were taken throughout the sculpin–dace transition area. Since few juvenile dace with full guts were preserved, overlap (Schoener 1970) in prey utilization was calculated for the valley reach by pooling the stomach contents of adult and juvenile fishes.

Metabolic Rates

We examined the temperature responses of both species in static respirometers to determine whether or not (1) sculpins were stressed at temperatures similar to those found in the dace-dominated riffles and (2) dace were stressed at temperatures similar to those found in the sculpin-dominated riffles. Speckled dace and riffle sculpin, captured by electroshocking riffle areas, were transported in aerated ice chests to the laboratory. They were held in flow-through tanks at a 12-h

TABLE 1. The proportion (P_i, P_j) number (No.), and catch per unit effort (CPUE) of speckled dace and riffle sculpin in a series of riffles in the valley reach of Deer Creek, August 11–13, 1980.

	Speckled Dace			Riffle Sculpin			
Riffle No.	P_i	No.	CPUE	P_j	No.	CPUE	Effort
1 (lowermost)	1.000	50	0.847	0.000	0	0.000	59
2	0.983	56	0.602	0.017	1	0.011	93
3	0.938	15	0.429	0.062	1	0.029	35
4	0.811	30	0.517	0.189	7	0.121	58
5	0.575	23	0.426	0.425	17	0.315	54
6	0.600	18	0.400	0.400	12	0.267	45
7	0.476	10	0.233	0.524	11	0.256	43
8	0.476	10	0.233	0.524	11	0.256	43
9	0.333	9	0.450	0.667	18	0.900	20
10	0.095	6	0.136	0.905	57	1.296	44
11	0.111	7	0.132	0.889	56	1.057	53
12 (uppermost)	0.013	1	0.018	0.987	79	1.411	56
Overall	0.465	235	0.390	0.535	270	0.448	603

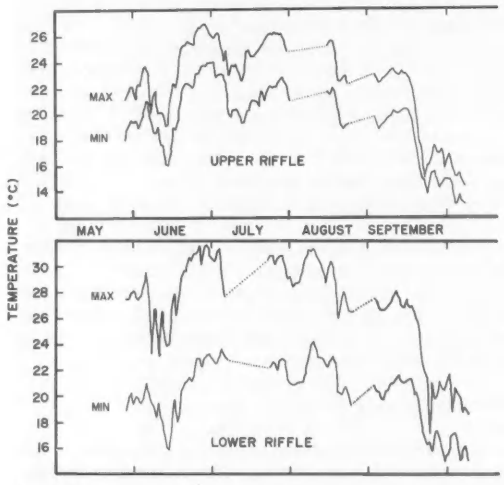

FIG. 1. Daily minimum and maximum stream temperatures in the upper and lower riffles in the valley reach of Deer Creek, Tehama County, California, 1981.

photoperiod for a minimum of 96 h before experiments. When required, temperature was adjusted via increases of $1°C \cdot d^{-1}$ or decreases of $0.5°C \cdot d^{-1}$. Fish were fed *Tubifex* and flake fish food daily except when fasted 24 hrs before respirometry trials. Routine metabolic rates were measured in sealed glass respirometer jars (0.65 L) immersed in a closed, dark, constant-temperature water bath. Six jars were used, allowing simultaneous measurements on five fish and one blank. After a minimum 3-h acclimation period, we took water samples (10 mL) for initial oxygen conditions, the flow was stopped and after 30–60 min a final sample of water was taken to determine the oxygen consumption rate in each jar. Oxygen concentrations were measured with a Beckman model 325814 oxygen macro-electrode and read on a Beckman model 160 physiological gas analyzer. Oxygen consumption ($mg \cdot g^{-1} \cdot h^{-1}$) was calculated for each fish, with corrections for the blank, temperature, and barometric pressure. A minimum of eight fish each were tested at 10, 15, 20, 25, and 27.5°C. Immediately following each run, standard lengths were recorded to the nearest millimeter and wet weights to the nearest 0.01 g.

CRITICAL VELOCITIES

We determined the critical velocities of speckled dace to test the hypothesis that dace were not excluded from the sculpin dominated riffles by the combination of temperatures and water velocities found there. Similar tests were not conducted on sculpins because they were able to cling to the bottom of the respirometers with their pelvic fins, and hence showed little response to increased current velocities. Critical velocities of speckled dace were measured in a swimming respirometer (vol. 3.5 L) immersed in a constant-temperature water bath (Brett 1964). Fish were introduced singly into the screened chamber for a minimum of 3-h acclimation at velocity of less than 1 $cm \cdot s^{-1}$. After acclimation the water velocity was increased 10 $cm \cdot s^{-1}$ every 10 min, with a 1-min rest interval between each test interval (Jones et al. 1974). The time at which the fish was pinned against the back screen was noted. The critical velocity was then determined by the following formula:

$$C.V. = V_p + \left[(V_f - V_p) \times \frac{t_f}{t_i}\right]$$

where V_p = previous water velocity ($cm \cdot s^{-1}$); V_f = final velocity ($cm \cdot s^{-1}$); t_f = time to fatigue at V_f (s); t_i = time between velocity increments (s) (Brett 1964). All fish tested occupied less than 10% of the cross-sectional area of the chamber; therefore, no adjustment was needed in the calculations (Jones et al. 1974). Fish were tested at 15, 20, and 25°C.

BEHAVIORAL INTERACTIONS

We used a laboratory stream tank designed as a riffle

TABLE 2. Focal point velocity ($cm \cdot s^{-1}$) and depth (cm) for speckled dace and riffle sculpin by reach in Deer Creek. Values are untransformed means ± 1 SD (sample size). Data from snorkeling observations.

	Speckled Dace		Riffle Sculpin	
	Valley Reach	Canyon Reach	Valley Reach	Canyon Reach
Focal point velocity	6.37±8.39 (43)	4.51±5.29 (41)	3.81±7.69 (32)	3.44±7.67 (91)
Focal point depth	1.14±1.58 (43)	5.90±12.49 (41)	0.06±0.35 (32)	2.35±9.81 (91)

TABLE 3. Microhabitat measurements for speckled dace and riffle sculpin by reach and size class in Deer Creek. Values are untransformed means ± 1 SD (sample size).

	Speckled dace				Riffle sculpin			
	Valley Reach		Canyon Reach		Valley Reach		Canyon Reach	
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
Mean water column velocity ($cm \cdot s^{-1}$)	28.6±23.4 (45)	43.3±37.1 (228)	9.5±11.0 (18)	20.8±15.4 (23)	46.7±44.2 (183)	46.3±40.5 (193)	26.5±24.2 (59)	30.5±20.5 (31)
Water column depth (cm)	26.0±14.6 (45)	25.7±13.1 (228)	45.7±43.9 (18)	64.9±16.6 (23)	32.4±15.4 (183)	35.3±15.7 (193)	55.9±16.8 (59)	64.8±25.6 (32)
Substrate[a]	6.3±0.29 (44)	6.3±0.46 (227)	6.1±0.84 (18)	6.1±1.03 (22)	6.4±0.54 (175)	6.4±0.74 (187)	6.1±0.77 (59)	6.2±0.89 (32)

[a]Substrate composition coded on modified Wentworth particle size scale (Bovee and Cochnauer 1977). See Fig. 5 description.

analog to examine behavioral interactions between dace and sculpin when refugia from high velocity water were in short supply. The stream tank had a race track configuration (1.2 × 2.4 m) in which water was driven by paddle wheels. Screens (6.5 mm square mesh) divided the tank into experimental and paddle wheel chambers. The bottom was covered with pea gravel for a depth of 5 cm. Four clay flower pot halves (8 cm diam) were placed on the gravel to provide limited refugia from the current. Current was turbulent and velocity varied throughout the experimental chamber from 5 to 30 $cm \cdot s^{-1}$. Water depth in the experimental chamber was maintained at 15 cm and temperature varied between 19.0 and 20.8°C.

The use of clay pots by dace varied in intensity and was scored on the basis of three behaviors. In the most intense use (Type I) dace occupied the pot for 30 s or more and were generally inactive and in contact with the substrate. In a less intense utilization (Type II) dace left the pot before 30 s and while in the pot were generally active and not in contact with the substrate. In the least intense utilization (Type III) dace did not enter the pot but held position in the water column downstream with a noticeable reduction in tailbeat frequency. Dace response was tested hierarchically for utilization Type I alone, utilization Types I and II combined, and utilization Types I, II, and III combined. The response of dace to sculpin occupancy was measured with zero to three sculpins occupying pots. Since the number of dace varied between observation intervals due to mortalities and escape from the experimental chamber, the utilization rates were adjusted for the number of dace present and the length of the observation interval (i.e. utilizations-$dace^{-1} \cdot min^{-1} \cdot 100$). Observations were made over 62 intervals, totaling 841 min. A multivariate model was used to fit the response of dace to a set of four dichotomous variables:

$$R = \alpha_1 S_1 + \alpha_2 S_2 + \alpha_3 S_3 + \alpha_4 S_4 + \mu$$

where the response (R) of dace was regressed on the occupancy status (S_i) of each of the four pots. The occupancy status of the ith pot was scored as one if occupied by a sculpin and as zero if not occupied. The response of speckled dace to the presence of riffle sculpin was examined by testing the regression coefficients α_i which are the dace utilization rates for each pot. The regression coefficients for dace utilization were established for each pot in the absence of sculpin. The coefficients were then adjusted for the presence of sculpin and the differences tested.

Results

FIELD STUDIES

Distribution and abundance — A significant negative correlation ($r_s = -0.8105$, df = 10, $P < 0.01$) existed between the relative abundances of the two species in the valley reach, as measured by catch per unit effort (Table 1). Speckled dace dominated riffles in the downstream (dace) zone of the reach, but in the upstream (sculpin) zone speckled dace occupied slower waters and the riffles were dominated by riffle sculpin. In the middle (sympatric) zone, dace and sculpin occurred throughout the riffles in nearly equal abundance. Riffle sculpin were nearly absent from the downstream zone.

Summer water temperature, which increased rapidly in the valley reach as the stream bed broadened and was less

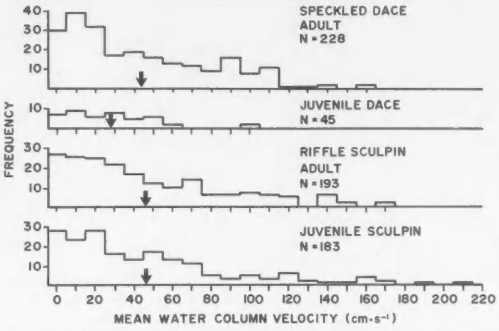

FIG. 2. Mean water column velocity above adult and juvenile riffle sculpin and speckled dace in Deer Creek. Arrows indicate mean velocities.

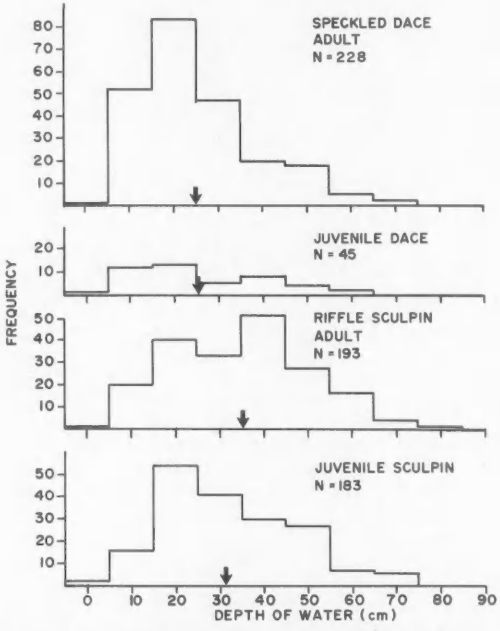

FIG. 3. Water column depths where adult and juvenile riffle sculpin and speckled dace were found in Deer Creek. Arrows indicate mean depths.

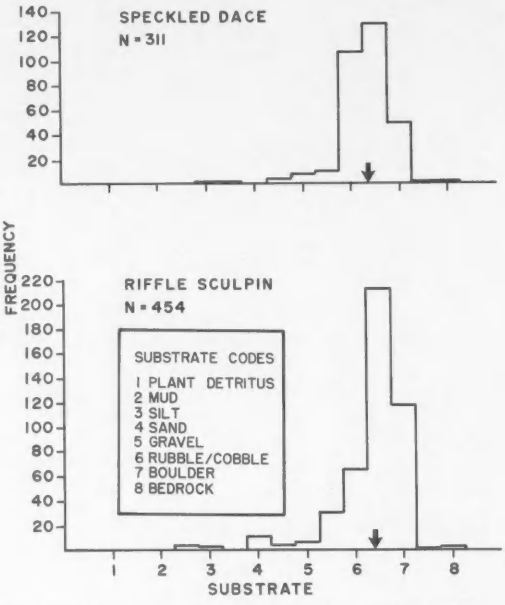

FIG. 4. Substrate type under riffle sculpin and speckled dace in Deer Creek. Substrate particle size is coded on a modified Wentworth scale (Bovee and Milhous 1978).

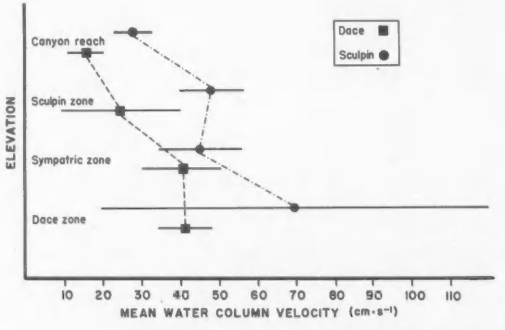

FIG. 5. Mean water column velocity utilization by riffle sculpin and speckled dace in three zones in the valley reach and in the canyon reach in Deer Creek. Horizontal lines are two standard errors.

protected from isolation by riparian canopy and canyon walls, appeared to limit the downstream distribution of sculpin. Morning temperatures were similar throughout the valley reach (20.8–21.0°C); however, the maximum afternoon temperatures recorded were 29.0°C in the upper riffle and 32.0°C in the lower riffle between August 11–13, 1980. Thus in summer the daytime water temperature in the upper riffle lagged behind and remained about 3 degrees cooler than in the lower riffle. Thermograph recordings in the upper and lower riffles indicated substantial differences in summer temperatures between the riffles dominated by sculpin and dace, respectively (Fig. 1). Water temperature was 7.0°C on January 8, 1981 throughout the valley reach, and both species were nearly equal in abundance in the lowermost riffles; however, both species were inactive and did not occupy fast waters but took refuge in the open cobble and boulder substrate at the edges of riffles. During the 1976–77 drought,

TABLE 4. Indices of overlap (Schoener 1970) in microhabitat in the valley reach between adult riffle sculpin and speckled dace, between adult and juvenile riffle sculpin, and the ratio of inter- to intraspecific overlap for adult sculpin. Upper limits of overlap are the mean ($\bar{x}$) and lower limits are the product (π) of the three variables.

	Adult dace and sculpin	Adult and Juvenile sculpin	Ratio (dace:sculpin)
Water column depth	0.6836	0.8337	0.8200
Mean water column velocity	0.8619	0.8623	0.9995
Substrate	0.7854	0.7902	0.9939
Maximum ($\bar{x}$)	0.7770	0.8287	0.9378
Minimum (π)	0.4628	0.5681	0.8146

sculpin were absent from the valley reach and dace occupied all of the riffles. The distributional pattern observed strongly suggests that the summer distribution of both species is related to temperature.

The modal class for focal point velocities was zero $cm \cdot s^{-1}$ for both species in both the canyon and valley reaches and means were slightly higher (Table 2); the focal point depth also had a mode of zero cm and a slightly higher mean for both species. Dace and sculpin were nearly always found at low focal point velocities usually under and behind rocks, even though the mean water column velocities above them were often quite high (Table 3). Underwater observations indicated that speckled dace were more active than sculpins and thus spent more time at higher focal point velocities.

Before making comparisons between species, we used two-way ANOVA to look for size-specific and reach-specific differences within species. For sculpins, mean water column velocities differed significantly by reach (F-ratio = 5.39; df = 1, 462; $P < 0.02$) but only marginally by size class (Fig. 2) (F-ratio = 2.91; df = 1, 462; $P < 0.09$). For dace the means were significantly different by reach (F-ratio = 17.7; df = 1, 310; $P < 0.0001$) and size class (F-ratio - 10.2; df = 1, 310; $P < 0.002$), with juvenile dace always in slower water. For both dace and sculpin, the mean water column velocities in the canyon reach were slower than velocities measured in the valley reach. The slower velocities in the canyon reach reflected the staircase character and limited extent of riffle habitat in the canyon area. Sculpins in the canyon reach occupied the short riffles and were also found in pools and runs which they rarely used in the valley reach. The maximum depth occupied by sculpin differed significantly by reach (F-ratio = 109.3; df = 1, 463; $P < 0.0001$) and size class (F-ratio = 3.88; df = 1, 463; $P < 0.05$). In both reaches, larger sculpins appeared to occupy deeper waters (Fig. 3); however, the slope for the regression of maximum depth on SL was not significant ($b = 0.096$, $r = 0.125$, $n = 314$, $P > 0.05$). For dace, maximum depth differed significantly by reach (F-ratio = 55.4; df = 1, 310; $P < 0.0001$) and size class (F-ratio = 13.6; df = 1, 310; $P < 0.0003$), and the regression of maximum depth on SL was significant ($b = 0.145$, $r = 0.149$, $n = 468$, $P < 0.01$). Young-of-the-year and yearling dace were restricted to the shallow margins of the stream. Both species used deeper water in the canyon reach (Table 3). Mean substrate values differed by reach for both dace (F-ratio = 5.37; df = 1, 307; $P < 0.021$) and sculpin (F-ratio = 7.61; df = 1, 449; $P < 0.006$) but size class differences were not significant (Fig. 4). The cobble-boulder substrates in the valley reach contained slightly more boulder than in the canyon reach; this difference reflected the faster water occupied by both species in the valley reach. Thus within-species differences were related to differences in resource availability between reaches and to some size-specific differences in microhabitat, especially for dace.

When dace and sculpin were compared by reach, two-way ANOVA indicated a significant difference between the mean water column velocities by species (F-ratio = 7.7; df = 1, 776; $P < 0.0056$) and reach (F-ratio = 29.7; df = 1, 776; $P < 0.0001$). The maximum depth utilized also differed significantly by species (F-ratio = 17.2; df = 1, 777; $P < 0.0001$) and by reach (F-ratio = 158.4; df = 1, 777; $P < 0.0001$). These differences appeared to be due primarily to the use by dace of slower water in the canyon reach (Table 3). When the comparisons were restricted to the valley reach, there were no significant differences in mean water column velocity between species (F-ratio = 2.32; df = 1, 646; $P > 0.128$) or size classes (F-ratio = 2.36; df = 1, 646; $P > 0.125$); however, sculpin used significantly deeper water (F-ratio = 22.1; df = 1, 646; $P < 0.0001$), but size class comparisons were not significant (F-ratio = 1.85; df = 1, 646; $P > 0.174$). Despite no overall differences in mean water column velocities in the valley reach, a closer comparison of mean water column velocities utilized by dace and sculpin in three zones in the valley reach and in the canyon reach indicated that the sculpins generally occupied faster waters (Fig. 5) but the differences were only significant where sculpin densities were high, i.e. in the sculpin zone and the canyon reach where the dace had been displaced to slower waters. Thus there was a shift by dace from riffles in the valley reach to slower waters in the canyon reach; this shift began and the transition was nearly complete in the valley reach. A two-way ANOVA comparing the substrate distributions for species by reach indicated no difference between species (F-ratio = 1.19; df = 1, 760; $P > 0.276$), but differences between reaches were significant (F-ratio = 13.3; df = 1, 760; $P < 0.0003$).

Despite some statistical differences between species and size classes in resource utilization, measures of niche overlap indicated a strong similarity between the microhabitats of adult dace and sculpin in the valley reach (Table 4). Intraspecific overlap between adult and juvenile sculpin was very high and overlap between adult dace and adult sculpin was nearly as high for all variables. The limits of the overall

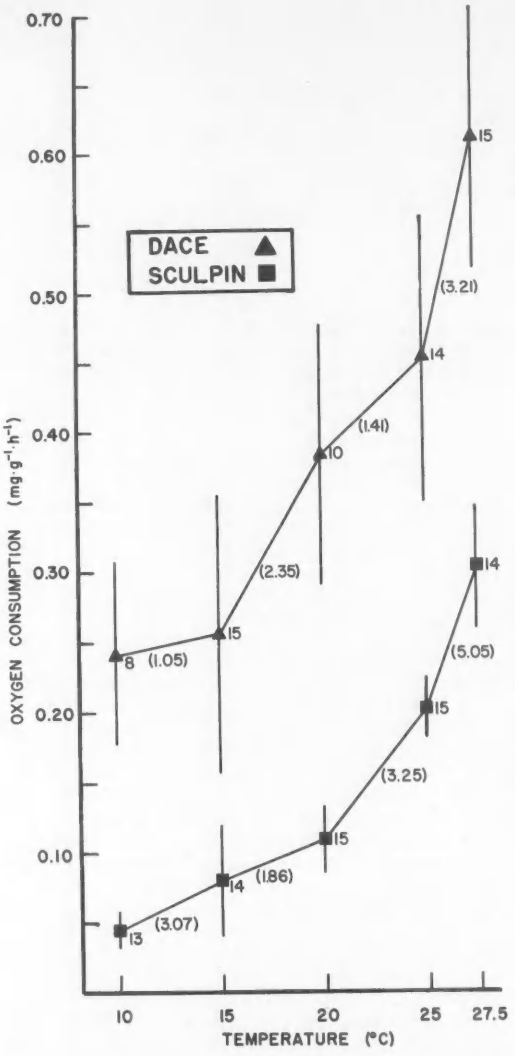

FIG. 6. Routine metabolic rates of riffle sculpin and speckled dace at five temperatures. Vertical lines are two standard errors, number in parentheses are Q_{10}s, and sample sizes are indicated next to means.

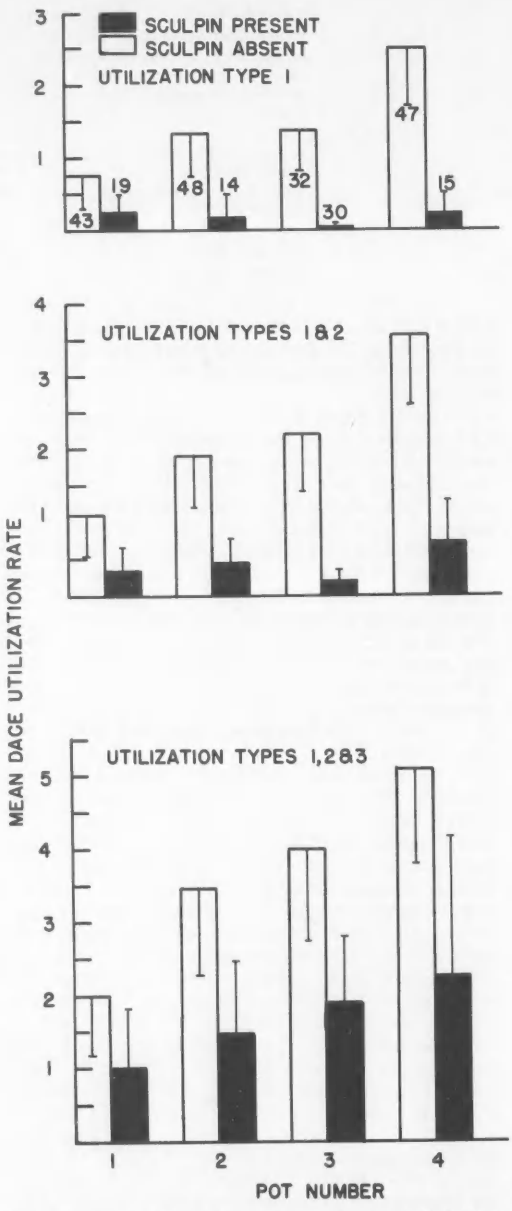

FIG. 7. The effect of sculpin on the utilization rates of individual pots by speckled dace. Bars indicate means, numbers indicate sample size, and vertical lines indicate two standard errors.

microhabitat similarity, estimated as the product for independent variables or as the mean for additive variables (May 1975), between adult sculpin and dace and between sculpin size classes ranged from moderate to high (Table 4). The ratio of inter- to intraspecific overlap for adult sculpin with adult dace and with juvenile sculpin was almost unity for two variables, mean water column velocity and substrate, and high for the third, maximum water depth (Table 4). Thus the overlap between dace and sculpin was nearly as high as between sculpin size classes.

Dietary overlap — The prey of dace and sculpin in the three zones of the valley reach were mainly riffle-dwelling benthic insects. In the lower series of riffles (the dace zone) where sculpins were rare, dace ($n = 22$) preyed primarily on *Hydropsyche* (65% by volume) and *Baetis* (16%). In the sympatric zone both dace ($n = 44$) and sculpin ($n = 37$) preyed heavily on *Hydropsyche* (42 and 67%, respectively) and on *Baetis* (31 and 9%, respectively). In the sculpin zone, *Isonychia* (54%) and *Hydropsyche* (32%) were utilized heavily by sculpins ($n = 49$). Dace ($n = 7$) from the sculpin zone preyed primarily on *Baetis* (54%) and *Hydropsyche* (6%). Differences in their diets were due to the relatively heavy reliance by dace on *Baetis* and by sculpin on *Isonychia*. *Isonychia* is probably too large to be eaten by dace, as the mouths of dace are much smaller than those of sculpins (Moyle 1976). Regression analysis of the head capsule widths of two major prey in the gut contents of both predators indicated that larger sculpins took larger *Baetis* ($r = 0.54$; $n = 17$; $P < 0.05$) and *Hydropsyche* ($r = 0.42$; $n = 88$; $P < 0.01$); however, there were no significant trends in prey size for dace. The high proportion of empty dace stomachs (22 of 27) hindered comparison of diets in the sculpin zone; however, from minimal samples the similarity appeared to be very slight (overlap = 0.09). In the sympatric zone, the diets were moderately similar (overlap = 0.50) and overall the similarity was only slightly higher (overlap = 0.56). Thus despite the evident abilities of sculpins to take larger prey than dace, the overall diets of sculpins and dace were moderately similar. A similar pattern of overlap of summer diets for dace and Pit sculpins (*C. pitensis*) has been noted elsewhere in Californa by Li and Moyle (1976), although their study also showed that the diet of dace shifted largely to algae in the fall.

Overall, the field studies indicated that competition was not the proximate factor causing the low abundance of sculpin in the lowermost riffles of Deer Creek during the summer months. This view is supported by the near absence of sculpin and the widespread occurrence of speckled dace in the riffles throughout the valley reach during the drought years 1976–77 and by our observations that sculpins were relatively more abundant in the lower reaches during the winter of 1980–81 when both species were inactive. Thus temperature appears to affect sculpin distribution. However, the presence of both species in the upper riffles (sculpin zone), but with the dace absent from fast water, indicated either that sculpins were competitively excluding dace from the fast water or that dace were unable to occupy riffles at colder temperatures for energetic reasons, regardless of the presence of sculpins. To examine these alternative hypotheses we conducted physiological and behavioral experiments.

Laboratory Studies

Static respirometry — Dace had higher and more variable routine metabolic rates than did sculpins at all temperatures (Fig. 6). Both the metabolic rates and the variabilities of the rates reflect basic differences in the activity patterns of the species. Sculpins were generally very inactive, even when stressed by high temperatures, whereas individual dace either swam continuously or rested in contact with the substrate in our static or flowing systems. We expected sculpin respiratory rates to increase rapidly due to stress at higher temperatures, but they did not increase faster in absolute terms than did dace rates. However, we noted that sculpin mortality increased rapidly at temperatures of 27.5°C and above. The relative increases, Q_{10}s, calculated for dace and sculpin over the interval studied (10–27.5°C) were 1.69 and 2.90, respectively, but sculpin Q_{10}s increased more dramatically between 20 and 27.5°C. This demonstrated that sculpin are generally more sensitive to temperature than dace, especially above 20°C (Fig. 6).

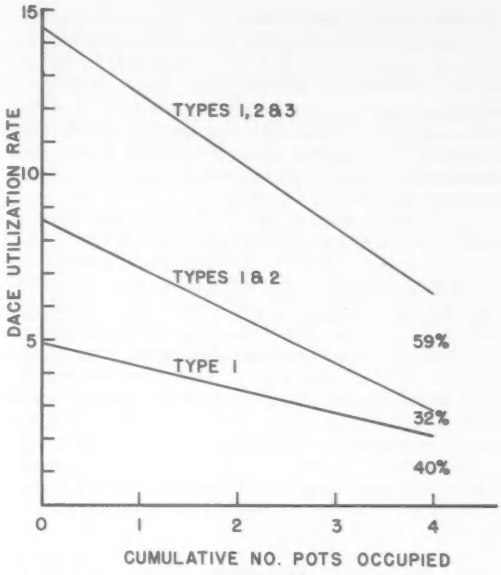

FIG. 8. The fitted model indicates that dace utilization declines as the proportion of pots occupied by sculpin increases. Percentages indicate projected residual utilization rates for each behavior type when all four pots are occupied by sculpin.

Critical velocity — The critical velocities ($\bar{x} \pm$ SE) achieved by dace were 52.7 ± 3.6, 49.3 ± 2.8, and 68.9 ± 2.7 cm·s^{-1} at 15, 20, and 25°C, respectively, and were far in excess of the focal point velocities (Table 2) and comparable to the mean water column velocities they generally utilized (Table 3). Since the swimming performance of dace increased with standard length (SL), analysis of covariance, with SL as a covariate, was used to test dace critical swimming velocities at three temperatures typical of the valley reach. The swimming performance of dace increased significantly with temperature (F-ratio = 9.9; df = 2, 39; $P < 0.001$), but performances at 15 and 20°C were not significantly different (t-test = 1.62; df = 25; $P > 0.11$). Dace critical velocities at the low temperatures were adequate to indicate an ability to maintain themselves in riffles at 15°C. Thus temperatures did not seem to be the factor causing their displacement to slower waters in the upper end of the reach.

Behavioral interactions — In the laboratory stream, dace

generally avoided clay flower pots occupied by sculpin. Dace occupying pots generally left when a sculpin entered; however, larger dace occasionally remained in or entered a pot occupied by sculpin. Dace were occasionally blocked, butted, or nipped when they attempted to enter a pot occupied by sculpin, and one instance of predation was observed. The aggressive behavior of sculpin toward dace was irregular but adequate to explain the apparent avoidance of sculpin by dace.

The utilization rates of dace were significantly higher in three of four pots when sculpin were absent (Fig. 7); however, the dynamics of the interaction are better explained by the multivariate model. When a pot was occupied by sculpin, dace utilization decreased in the occupied pot but generally increased in the unoccupied pots. However, the model indicated that as the cumulative number of sculpin occupying pots increased the total utilization by dace decreased (Fig. 8). Thus the behavior of dace and sculpin in the laboratory stream reflected the same pattern observed in the field: dace utilization of limited refugia was negatively correlated with sculpin abundance in the microhabitat. Figures 7 and 8 also indicated that the more intense uses (Types I and II) of clay pots by dace were the most severely affected by the presence of sculpin.

Discussion

Our analysis indicated that speckled dace and riffle sculpin in Deer Creek segregated on the basis of competitive interactions that were moderated by temperature. Summer temperatures probably exceeded limits tolerable to sculpins in the lowest reaches of the stream, but maximum daily temperatures and temperature variation decreased steadily in an upstream direction. Sculpin abundance also increased in an upstream direction whereas dace abundance decreased, at least in fast water. The mechanism of dace displacement appeared to be their avoidance of riffle areas occupied by sculpin, and laboratory observations showed that aggression by sculpin and occasional predation were the immediate causes. Pugnacious sculpins occupying refugia were able to deny shelter to dace at little cost energetically to themselves; however, displaced dace must expend considerable energy to regain and hold position in the riffles. Therefore, if the abundance of sculpins was high in a riffle, the abundance of dace was likely to be low. Presumably, the riffles were the preferred habitat of both species because they contain the highest concentrations of prey organisms (Hynes 1970) and because the fast flowing water and the coarse substrate provided cover from predators.

Most previous studies in temperate waters that have convincingly demonstrated that competitive interactions between fish species can affect choice of microhabitat have dealt with morphologically similar species (Johannes and Larkin 1961; Nilsson 1967; Calwalladder 1975; Larson 1980; Hixon 1980). The general lack of good evidence of competitive interactions between dissimilar stream fishes (Moyle 1977; Holey et al. 1979; Brown and Moyle 1981) has not kept fisheries managers from frequently assuming that competition between dissimilar species is a major factor influencing the structure of freshwater fish communities. This assumption has led to the widespread use of ichthyocides to eliminate undesirable species that are "competing" with desirable species (Eschmeyer 1975), despite the rarity of studies that have been designed to determine whether or not competition actually exists. On the other hand, fisheries managers charged with determining optimal flow regimes for fisheries purposes in regulated streams generally ignore the role of competition in stream fish communities. This is largely because the principal models and techniques currently in use assume that each species reacts to the physical and chemical characteristics of its environment independently of the other species present (Bovee and Cochnauer 1977). Our study suggests that the use of broad assumptions about the role of competition in stream fish communities as the basis for management decisions is likely to lead to erroneous decisions. It also suggests that it is important to understand how biological interactions are influenced by physical and chemical factors. If we had not examined the warmer reaches of Deer Creek during our initial surveys, it is unlikely that we would have suspected that microhabitat utilization by dace was influenced by competition from sculpins or that this interaction was mediated by temperature.

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Immunogenic Potential of Growth Products Extracted from Cultures of *Aeromonas salmonicida* for Brook Trout (*Salvelinus fontinalis*)

ROCCO C. CIPRIANO

U.S. Fish and Wildlife Service, National Fish Health Research Laboratory, Box 700, Kearneysville, WV 25430, USA

CIPRIANO, R. C. 1982. Immunogenic potential of growth products extracted from cultures of *Aeromonas salmonicida* for brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. 39: 1512 – 1518.

Growth products from virulent (3.93 and 3.101), an avirulent (3.10), and an atypical strain (3.111) of *Aeromonas salmonicida* yielded four protein containing fractions (designated fractions 1, 2, 3, 4) following chromatography on DEAE Sephadex A-25 of crude material that was precipitated from broth culture supernatants with $(NH_4)_2SO_4$ and ethanol. Vaccination trials, in which each of the four fractions from a virulent and an avirulent strain were injected intraperitoneally at a dose of 5 μg protein into brook trout (*Salvelinus fontinalis*) indicated that only fraction 4 consistently protected trout from experimental challenges. Immunizing fish with fraction 4 that was emulsified in Freund's incomplete adjuvant also protected trout from challenge but did not enhance protection. Additional brook trout that were immunized by injection with fraction 4 derived from either of two virulent, an avirulent, or an atypical strain of *A. salmonicida* were also protected from contact challenge with a different challenge strain. Fraction 4 was partially characterized as a glycoprotein; the protein subunit fraction had an approximate molecular weight of 66 000 daltons. Rabbit antiserum prepared against fraction 4 reacted on agar gel diffusion plates to form a single precipitin band with the homologous fraction 4 antigen but this antiserum did not cross react with either purified preparations of bacterial endotoxin or A-layer protein.

Key words: *Aeromonas salmonicida*, *Salvelinus fontinalis*, growth products, fraction 4, glycoprotein, virulent, avirulent, atypical strains, contact experimental challenge

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Les produits de croissance d'une lignée virulente (3,93 et 3,101), avirulente (3,10) et atypique (3,111) d'*Aeromonas salmonicida* donnent quatre fractions contenant des protéines (que nous désignons 1, 2, 3, 4) après chromatographie sur Sephadex DEAE A-25 du matériel brut précipité par $(NH_4)_2SO_4$ et éthanol du liquide surnageant des cultures sur bouillon. Des expériences de vaccination, au cours desquelles chacune des quatre fractions provenant d'une lignée virulente et avirulente ont été injectées par voie intrapéritonéale, à une dose de 5 μg de protéines, dans des ombles de fontaine (*Salvelinus fontinalis*), indiquent que seule la fraction 4 protège invariablement les ombles contre les attaques expérimentales. L'immunisation de poissons à l'aide de la fraction 4 émulsifiée dans l'adjuvant incomplet de Freund les protège également contre les attaques, sans toutefois accroître cette protection. D'autres ombles de fontaine immunisés par injection d'une fraction 4 dérivée de l'une ou l'autre de deux lignées virulente, avirulente ou atypique de *A. salmonicida* sont également protégés contre une attaque par contact d'une lignée différente. La fraction 4 est caractérisée partiellement comme glycoprotéine; la fraction subunitaire protéique a un poids moléculaire d'environ 66 000 daltons. Un antisérum de lapin préparé contre la fraction 4 réagit sur plaques diffusantes de gélose pour former une bande unique de précipitine avec l'antigène homologue de la fraction 4, mais cet antisérum ne réagit ni avec des préparations purifiées d'endotoxine bactérienne ni avec les protéines de la couche A.

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FURUNCULOSIS is a major disease of intensively cultured fishes. Efforts to control the etiologic agent, *Aeromonas*

salmonicida, include avoidance, prevention, development of disease resistant fishes, chemotherapy, and vaccination. Oral immunization to control furunculosis was successful in early tests (Duff 1942), but the protection produced by orally delivered bacterins of *A. salmonicida* has since been inconsistent (Paterson 1981). A comparison of bacterins and delivery methods (Udey and Fryer 1978) confirmed reports that protection was best produced by injecting fish with formalinized cells emulsified in an adjuvant (Krantz et al. 1964a,b; Paterson and Fryer 1974). Because injected bacterins also produced humoral agglutinating antibodies, these agglutinins were considered to be indicators of a protective immune response. Consequently, the kinetics of the agglutinin response against *A. salminicida* was studied (Maisse and Dorson 1976; Ikeda 1978a,b), but even fish with strong humoral antibodies were not necessarily protected from experimental challenges (Michel 1979; Cipriano 1982).

Because it is impractical to immunize large numbers of small fish by injection, furunculosis bacterins were administered by hyperosmotic infiltration (Antipa and Amend 1977) and flush exposure (Anderson et al. 1979). However, these methods of vaccination were not as successful against *A. salmonicida* as they proved to be against *Vibrio anguillarum* (Lannan 1978; Antipa et al. 1980) and *Yersinia ruckeri* (Anderson and Dixon 1980). Recent studies indicated that oral vaccination against furunculosis is practical and that a cellular immune response may indicate more protection against this bacterium than levels of humoral or mucous antibodies (Smith et al. 1980).

Since the work of Klontz et al. (1966), attention has focused on the ability of extracellular products from *A. salmonicida* to induce pathogenic effects in fishes (Fuller et al. 1977; Cipriano 1980; Ellis et al. 1981). However, little information on the immunogenic nature of these products exists. In the present study, four chromatographic fractions derived from the growth products of several strains of *A. salmonicida* were examined for their immunogenicity in trout. This report summarizes those findings.

Materials and Methods

Four strains of *A. salmonicida* (Table 1) were obtained from the culture collection at this laboratory. Isolates were thawed, seeded onto Brain Heart Infusion (BHI) agar (Difco) slants, and incubated for 24 h at 20°C. The agar slant cultures were then transferred to 100-mL flask cultures of BHI broth that were incubated at 20°C for 24 h on a rotary shaker at 200 rpm. These cultures were then inoculated into 2 L of aerated BHI broth and incubated for an additional 5 d at 20°C. Cells were centrifuged from each of the broth cultures at 3 896 *g* for 30 min at 4°C and crude growth product materials were prepared by precipitating proteins from the spent culture media with $(NH_4)_2SO_4$ (0.8 saturation) and ethanol as described by Cipriano et al. (1981). Samples of the resulting preparations were then resolved into four protein-containing fractions by elution from DEAE Sephadex A-25 columns using a discontinuous NaCl gradient as described by Cipriano (1980). Each of the four fractions that were resolved from the crude materials (designated fractions 1, 2, 3, 4) was adjusted in phosphate buffer to contain 50 μg protein/mL (Bradford 1976).

Each of the four fractions from the virulent strain 3.101 was screened initially to determine their capacity to immunize fish against experimental challenge. Brook trout (*Salvelinus fontinalis*) averaging 51 g, obtained from the White Sulphur Springs (West Virginia) National Fish Hatchery, were divided into groups containing 30 fish that were maintained in 12.5°C spring water. Each fish per group was injected intraperitoneally (i.p.) with 0.1 mL (5 μg protein) of a respective fraction. Because no proteins were precipitated from BHI broth that was not inoculated with bacteria under the conditions described here, we concluded that each of the proteins resolved from inoculated media were bacterial components. Therefore, trout that were injected with 0.1 mL of the same phosphate buffer in which the bacterial fractions were diluted, served as control fish. After 21 d, each group was then challenged for 60 s by exposure to 10^9 viable cells per mL of culture of *A. salmonicida*, 3.101. Challenges were conducted at 12.5°C and 2 L of a 48-h broth culture was used. Subsequent mortality was recorded and confirmed by direct flourescent antibody examination of the kidney tissue for *A. salmonicida* (Bullock et al. 1980). After 14 d, the protective nature of each fraction was determined and compared to the mortality of the control groups. Protection was determined to be significant by chi-square analysis ($P < 0.05$).

To determine if these initial results were reproducible, the chromatographic fractions derived from the avirulent strain 3.10 were then screened in additional trout. All conditions of this test were similar to those described for screening the fractions from strain 3.101.

After these tests were completed, it was observed that fraction 4 protected trout from experimental challenge. Subsequent groups of 30 trout were then injected i.p. with fraction 4 emulsified in adjuvant to determine if this would further enhance protection. Each fish per group was injected i.p. with 0.2 mL of an equal mixture of fraction 4 (5 μg protein) emulsified in Freund's incomplete adjuvant. One group of trout was injected with fraction 4 derived from strain 3.101, another group was immunized with fraction 4 derived from strain 3.10, and a third group of trout injected i.p. with 0.2 mL of phosphate buffer in adjuvant served as controls. Fish were held for 21 d before each of the groups was challenged as already described. All other conditions of this experiment were similar to those previously mentioned in screening studies.

Another study was then conducted to determine if fraction 4 derived from several sources would protect fish from another challenge isolate and to also determine if this protection could be produced in a different population of brook trout. Brook trout (60 g) were obtained from the Paint Bank (Virginia) National Fish Hatchery and maintained 20 per group in 12.5°C spring water. Each fish was immunized by i.p. injection of 0.1 mL (5 μg protein) of fraction 4 derived from medium precipitates of typical strains 3.10, 3.93, 3.101, and an atypical strain 3.111 that was isolated from diseased goldfish. Trout that were injected with 0.1 mL of phosphate buffer served as controls. After 21 d all fish were challenged by a 60 s exposure to 10^8 cells of challenge strain 3.93. Mortality due to *A. salmonicida* was recorded and confirmed

TABLE 1. Isolates of *Aeromonas salmonicida* used in this study.

Identification number	Host	Source	LD50 in brook trout (cells/fish)
3.10	*Salvelinus fontinalis*	Bellefonte, PA.	$>10^7$
3.93	*Salmo salar*	Craig Brook, ME.	1.4×10^1
3.101	*S. fontinalis*	Kearneysville, WV.	3.8×10^1
3.111	*Carassius auratus*	Thurmont, MD.	3×10^2

TABLE 2. Total protein estimates of the soluble growth components obtained from isolates of *Aeromonas salmonicida*.

Isolate	Growth component (μg protein/mL) 1	2	3	4
Avirulent (3.10)	1090	822	1209	87
Virulent (3.93)	1255	966	843	31
Virulent (3.101)	409	485	409	35
Atypical (3.111)	1086	664	777	30

for 14 d, and protection amongst the groups was determined as previously described.

Because our results indicated that fraction 4 protected trout against experimental challenge, further studies were performed to partially characterize this bacterial component. Samples of fraction 4 (10 μL) from the virulent strain 3.101 and the avirulent strain 3.10 were electrophoresed in 10% polyacrylamide gels (Laemmli 1970). Each sample and molecular weight standards (Sigma) were subjected to 8 mA of current per gel for 4 h. Individual gels were stained for protein with Coomassie Brilliant Blue (Chrambach et al. 1967), for carbohydrates using the Schiff-Nadi method as modified by Fuller et al. (1977) and for lipoprotein using lipid crimson (Williams and Chase 1968).

Protein content of fraction 4 sample was assayed by the method of Bradford (1976) using bovine plasma gamma globulin as a standard. Carbohydrate determinations were made by the phenol-sulfuric acid method (Nowotny 1969) using dextran as a standard.

A rabbit antiserum that was prepared against fraction 4 from the virulent isolate 3.101 was reacted in agar gel diffusion plates (Ouchterlony 1958) against the homologous

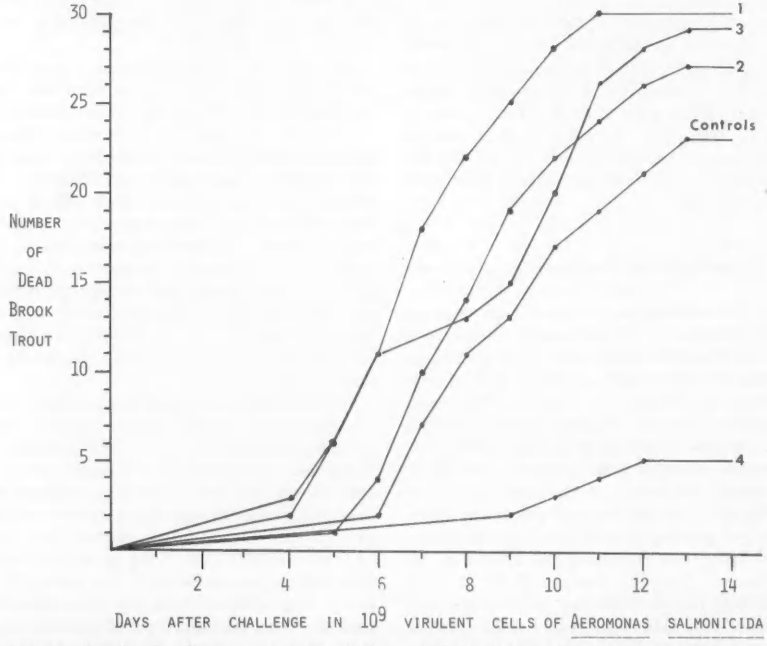

FIG. 1. Results of preliminary vaccination trials in which brook trout (*Salvelinus fontinalis*) were immunized with growth fractions 1, 2, 3, and 4 derived from strain 3.101 of *Aeromonas salmonicida* and then challenged by a contact exposure to homologous viable cells.

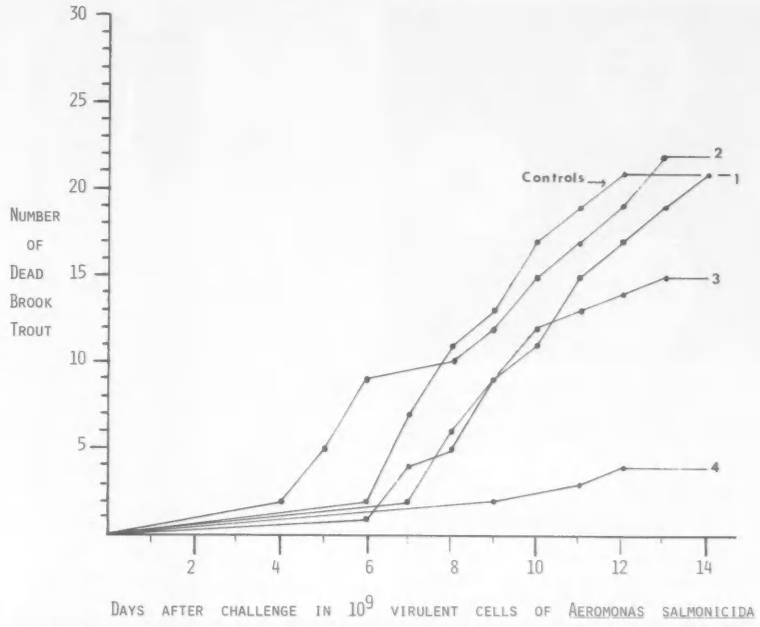

FIG. 2. Results obtained when brook trout (*Salvelinus fontinalis*) were immunized with growth fractions 1, 2, 3, and 4 derived from an avirulent strain, 3.10, of *Aeromonas salmonicida* and subsequently challenged by contact exposure to the virulent strain 3.101.

fraction 4, purified endotoxin (obtained from W. D. Paterson) and purified A-layer protein (obtained from W. W. Kay). The antiserum used for these assays was prepared by injecting a New Zealand White rabbit intramuscularly with 1.0 mL of fraction 4 (50 μg protein) from strain 3.101 that was emulsified with 1.0 mL of Freund's complete adjuvant. After 28 d, a booster injection of 0.5 mL of fraction 4 was delivered intravenously and the serum was tested for precipitin antibodies after 14 d and the serum was stored at −70°C.

Results

Four growth products or fractions were resolved from the medium precipitates of each *A. salmonicida* strain. Proteins were eluted from DEAE Sephadex A-25 columns at 0, 0.3, 0.6, and 1.2 mol/L NaCl and these were designated fractions 1, 2, 3, and 4, respectively (Table 2). Elution profiles were similar to those already described by Cipriano et al. (1981).

The results of preliminary vaccination trials in which trout were immunized with the fractions from the virulent strain 3.101 indicated that only those fish injected with fraction 4 resisted experimental challenge. Trout injected with fraction 1 had a 100% mortality, those injected with fraction 2 had a 90% mortality, those injected with fraction 3 had a 97% mortality, those injected with fraction 4 had a 17% mortality, and control fish sustained a 77% mortality. Mortality among fish injected with fractions 1, 2, and 3 derived from strain 3.101 were higher than nonvaccinated controls (Fig. 1). Only those fish immunized with fraction 4 showed a statistically significant (χ^2 (1 df) 21.7; $P < 0.001$) level of protection.

Subsequent vaccination attempts using the growth fractions derived from the avirulent strain 3.10 indicated that results obtained during preliminary vaccination trials were reproducible even when another strain of *A. salmonicida* was used to derive the growth fractions. Trout that were injected with fraction 1 from strain 3.10 had a 70% mortality, those injected with fraction 2 had a 71% mortality, those injected with fraction 3 had a 50% mortality, those injected with fraction 4 had a 10% mortality, and control fish had a 71% mortality (Fig. 2). As observed in prior tests with strain 3.101, fraction 4 from the avirulent strain 3.10 produced a statistically significant (χ^2 (1 df) 21.99; $P < 0.001$) protection whereas other fractions did not.

Although trout immunized with fraction 4 emulsified in Freund's incomplete adjuvant were protected from experimental challenge, the protection was similar to those fish immunized with fraction 4 alone. However, these results enforced the reproducibility of protecting fish against experimental furunculosis by immunization with fraction 4.

In these studies, groups of brook trout immunized by i.p. injection of fraction 4 derived from either the avirulent strain 3.10 or the virulent strain 3.101 had a similar mortality (10%), whereas the control group sustained a 71% mortality (Fig. 3). Protection afforded either group were, therefore, similar (χ^2 (1 df) 27.49; $P < 0.001$).

The final vaccination study indicated that even a different

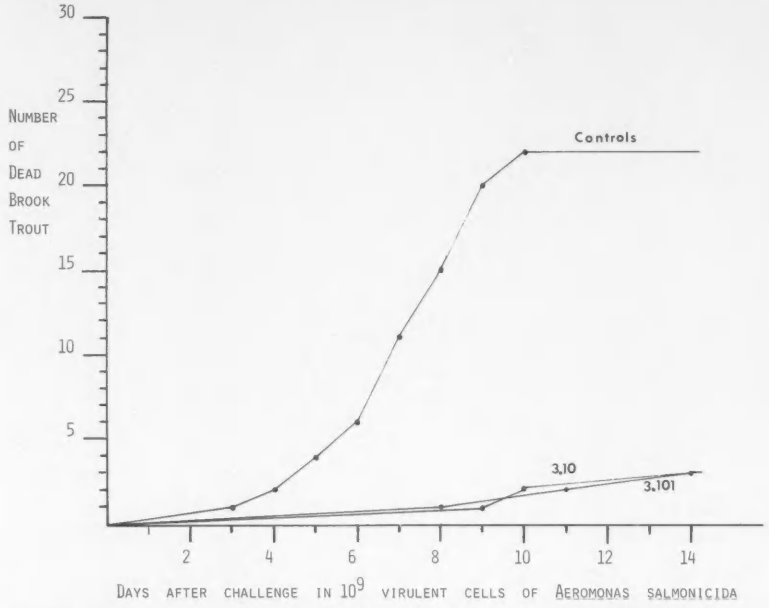

FIG. 3. Results of vaccination trials in which brook trout (*Salvelinus fontinalis*) were immunized by intraperitoneal injection of 5 μg protein fraction 4 emulsified in Freund's incomplete adjuvant derived from virulent strain 3.101, and avirulent strain 3.10 and subsequently challenged by contact exposure to viable cells of *Aeromonas salmonicida* 3.101.

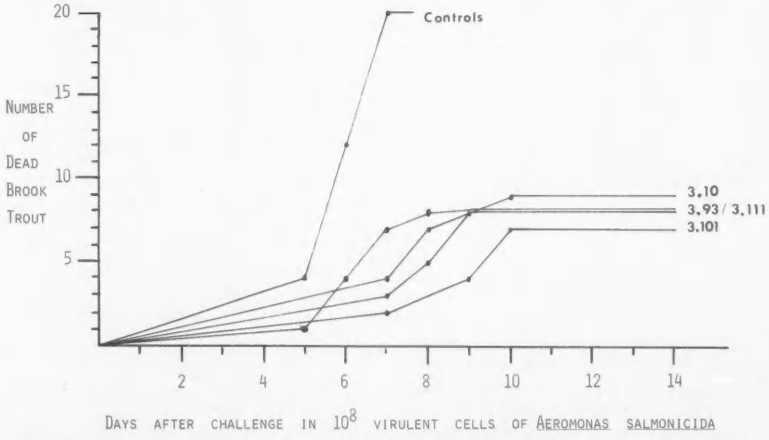

FIG. 4. Results of vaccinating brook trout (*Salvelinus fontinalis*) by injections of 5 μg protein of fraction 4 derived from strains 3.10, 3.93, 3.101, and 3.111 and subsequently challenged by a contact exposure to viable cells of strain 3.93.

population of fish immunized with fraction 4 derived from several strains withstood a challenge from another virulent isolate (3.93). The group of trout immunized by injection of fraction 4 from the avirulent strain 3.10 had a 45% mortality, those immunized with fraction 4 from either the virulent strain 3.93 or the atypical strain 3.111 had a 40% mortality, those immunized with fraction 4 from the virulent strain 3.101 had a 35% mortality, and control fish had a 100% mortality

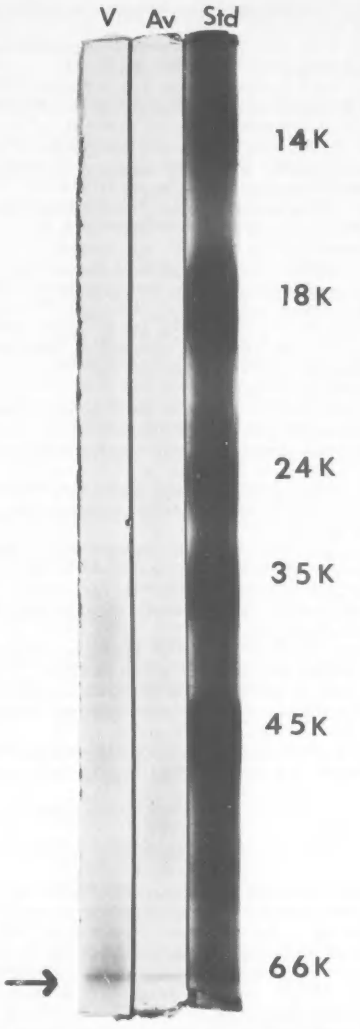

FIG. 5. Electrophoresis of fraction 4 derived from virulent strain 3.101 (V) and an avirulent strain 3.10 (Av) of *Aeromonas salmonicida* in 10% SDS-polyacrylamide gels stained with brilliant Coomassie blue and compared to standard (Std) reference proteins.

(Fig. 4). The level of protection afforded each of the groups of fish vaccinated with fraction 4 was significant (χ^2 (1 df) 15.7, 17.4, 19.3; $P < 0.001$).

Characterization studies indicated that fraction 4 was a glycoprotein. Fraction 4 from both the virulent strain 3.101 and the avirulent strain 3.10 showed a single protein band in 10% polyacrylamide gels with a migration equivalent to that of bovine plasma albumin (Fig. 5). The molecular weight of the protein subunit was therefore estimated to be 66 000 dal-

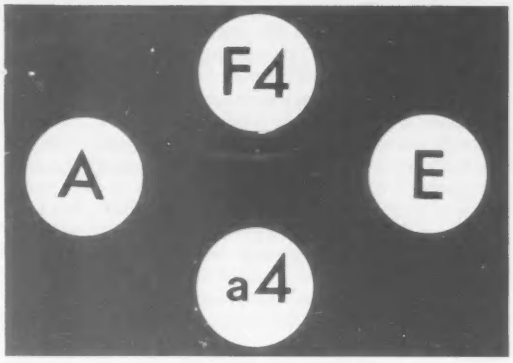

FIG. 6. Agar gel diffusion of a rabbit antiserum against fraction 4 from *Aeromonas salmonicida* strain 3.101 (a4) against the homologous fraction 4 antigen (F4), purified endotoxin (E), and purified A-layer protein (A).

tons. A carbohydrate band that migrated midway between bovine plasma albumin and ovalbumin (45 000 molecular weight) was also present in other gels but no lipoprotein bands were detected. Analysis of samples of fraction 4 from strains 3.10 and 3.101 indicated that there was a ratio of 1 part protein to 1.2 parts carbohydrate.

The agar gel diffusion studies also indicated that rabbit antiserum to fraction 4 formed a single precipitin band against the homologous fraction 4 antigen but this antiserum did not react with either purified preparation of endotoxin or A-layer (Fig. 6).

Discussion

The results presented in this study showed that the growth material found in spent culture supernatants of *A. salmonicida* consists of at least four protein groups and that only fraction 4, which is eluted from DEAE Sephadex A-25 with 1.2 mol/L NaCl, consistently protected trout from experimental challenges. This fraction was immunogenic in brook trout regardless of the virulence of the strain from which it was derived. It was also observed that fraction 4 derived from strain 3.111, an atypical *A. salmonicida* isolated from an outbreak of goldfish ulcer disease at a local hatchery, was immunogenic and protected trout from experimental challenges with virulent etiologic agents of typical furunculosis.

Researchers have indicated previously that, although protection could be afforded to fish immunized and challenged with the same strain of *A. salmonicida*, this protection broke down when a different strain of the bacterium was used to challenge fish (Smith et al. 1980). The work presented in the present study suggests that the inability to protect immunized fish against more than one challenge strain of *A. salmonicida* may result from producing an immune response against an immunogen that is not common to all strains. However, trout that were immunized with fraction 4 from several strains of *A. salmonicida* resisted subsequent challenges using either of two different virulent strains of the bacterium. This indicates

that fraction 4 is a significant protective antigen and is common to all strains used in this study.

Cipriano et al. (1981) showed that fraction 4 produced in vitro cytotoxicity but did not induce apparent gross pathological changes when it was injected into fish, and that it neither possessed leukocytolytic or proteolytic activities. The agar gel diffusion and molecular weight determinations conducted on fraction 4 in the present study further suggest that this component is neither related to the endotoxin or outer membrane A-layer protein produced by *A. salmonicida*. In a positive sense, it can be said that fraction 4 is a glycoprotein with an approximate protein sub-unit molecular weight of 66 000 daltons that is common to strains of this bacterium regardless of their virulence. However, further studies are needed to understand its role in the structural composition of this bacterium.

Acknowledgments

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Histology and Prevalence of X-Cell Lesions in Atlantic Cod (*Gadus morhua*)

C. M. MORRISON, G. SHUM, R. G. APPY[1], P. ODENSE, AND C. ANNAND

Department of Fisheries and Oceans, Fisheries and Environmental Sciences, Halifax Laboratory, Halifax, N.S. B3J 2S7

MORRISON, C. M., G. SHUM, R. G. APPY, P. ODENSE, AND C. ANNAND. 1982. Histology and prevalence of X-cell lesions in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 39: 1519–1530.

The prevalence of X-cell lesions in Atlantic cod (*Gadus morhua*) from the Canadian Atlantic was similar to that in German Bight and lower than their prevalence in *G. macrocephalus* off the west coast of Canada. The lesions, which are now believed to be xenomas composed of X-cell parasites and host cells were different from those described by other authors in that the pseudobranchs could always be seen on the exposed surface of the lesion, and were not infiltrated by X-cells. Sometimes the X-cell lesion was separate from the pseudobranch. Most of the X-cells in the lesion appeared to be degenerate, but areas of normal X-cells with distinctive features could always be found. No phagocytes were seen in the X-cell lesion, although a cellular host reaction to microsporidian and other parasites was often seen in and around the pseudobranch. It is suggested that the envelope cells, which are fibroblast-like, may represent a host response to the X-cells.

Key words: pseudobranch tumor, X-cells, Atlantic cod, *Gadus morhua*, Canadian Atlantic, epizootiology, histology, ultrastructure

MORRISON, C. M., G. SHUM, R. G. APPY, P. ODENSE, AND C. ANNAND. 1982. Histology and prevalence of X-cell lesions in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 39: 1519–1530.

La prédominance de lésions par cellules-X chez la morue (*Gadus morhua*) de l'Atlantique canadien est identique à celle observée dans le German Bight et inférieure à celle de *G. macrocephalus* du large de la côte occidentale du Canada. Ces lésions, que l'on considère maintenant comme xénomes composés de cellules-X parasites et de cellules hôtes, diffèrent de celles que d'autres auteurs ont décrites, en ceci que les pseudobranchies sont toujours visibles à la surface exposée de la lésion et ne sont pas envahies par les cellules-X. Parfois, les lésions causées par les cellules-X sont séparées de la pseudobranchie. La plupart de ces cellules dans la lésion semblent dégénérées, mais on peut toujours trouver des zones de cellules-X normales à caractères distinctifs. Nous n'avons observé aucun phagocyte dans la lésion par cellules-X, bien qu'une réaction de l'hôte cellulaire à la microsporidie et autres parasites soit souvent visible à l'intérieur et autour de la pseudobranchie. Nous émettons l'hypothèse que les cellules-enveloppe, ressemblant à des fibroblastes, peuvent représenter une réaction de l'hôte aux cellules-X.

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X-CELL lesions have previously been termed pseudobranch tumors, composed of two cell types, the tumor (Lange 1973) or X-cells (Alpers et al. 1977), surrounded by sustentacular (Lange and Johannessen 1977) or envelope cells (Alpers et al. 1977). However, there is now increasing evidence to suggest that the X-cells are parasites (Dawe 1981), in which case the X-cell lesion is a xenoma of parasitic X-cells surrounded by envelope cells of host origin. X-cell lesions of gadoid fishes have been reported and described from a variety of northern marine localities. They have been described in Atlantic cod, *Gadus morhua*, off Norway (Lange and Johannessen 1977) and in the German Bight area (Watermann and Dethlefsen 1980), from Pacific cod, *Gadus macrocephalus*, off British Columbia (Wellings 1969; Stich et al. 1976; Alpers et al. 1977) and from Pacific cod and walleye pollock, *Theregra chalcogramma*, in the Bering Sea (McCain et al. 1979). Despite the potential importance of these lesions as pollution indicators or as a cause of mortality in juvenile fish (Stich et al. 1976), no studies on them exist for the northwest Atlantic.

The present study extends the preliminary report of Morrison et al. (1979) and describes the prevalence and morphology of X-cell lesions in Atlantic cod in the Canadian

[1]Present address: University of Guelph, Department of Zoology, Guelph, Ont. N1G 2W1.

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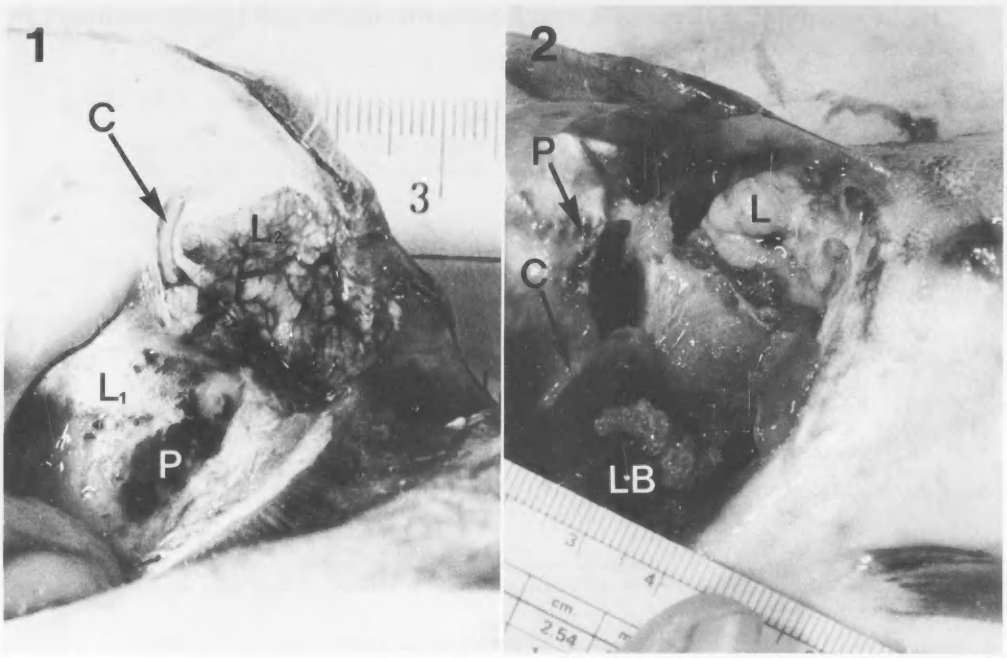


FIGURES 1–2

FIG. 1. Ventral surface of cod with bilateral X-cell lesion. This photograph shows the lesion on the left side of the fish. The bulk of the lesion (L_1) is in its usual position in the pre-oesophageal depression, with the pseudobranch (P) intact on its surface. However part of the lesion (L_2) has extended to the outer edge of the operculum where deformation is occurring. A copepod *Clavella* sp. (C) is embedded in the lesion (Scale mm); FIG. 2. Ventral surface of cod with bilateral X-cell lesions. The left lesion (L) is completely separate from the pseudobranch (P), and extends back to the head kidney region. The copepods *Clavella* sp. (C) and *Lernaeocera branchialis* (LB) are attached to the gills (Scale mm).

FIGURES 3–4

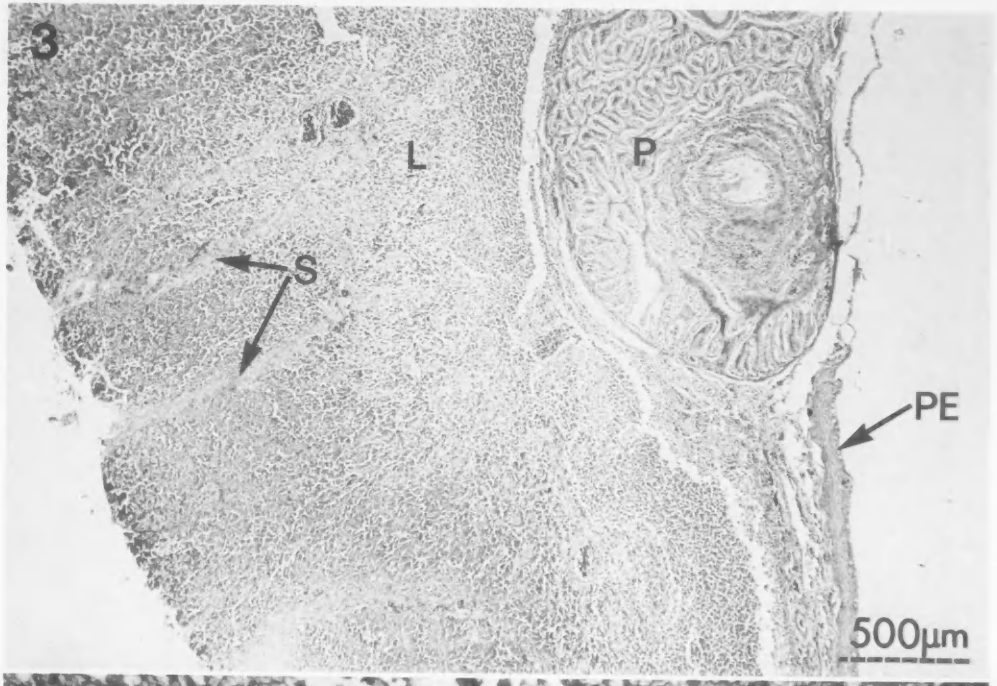
FIG. 3. Light micrograph of cross section through pseudobranch (P), lesion (L) and pharyngeal epithelium (PE). The pseudobranch retains a compact form, and normal cellular structure. It is separated from the X-cell lesion by a layer of connective tissue. Connective tissue septa (S) which contain capillaries can be seen extending through the X-cell lesion. The lesion fills the whole of the pre-esophageal fossa. The base of the lesion, to the left of the figure, would have been adherent to the floor of the fossa before excision of the lesion; FIG. 4. Microsporidian cyst (M) in cod X-cell lesion. Capillaries (C) can be seen throughout the lesion. Unstained cells equivalent to Alper's Stage III cells (111) can be seen surrounding the capillaries, whereas larger Stage II cells (11) with a basophilic granular cytoplasm can also be seen.

FIG. 5. Electron micrograph of type I X-cells (X), and envelope cells (E) which surround collagen bundles (CB) as well as X-cells. The X-cells show the typical features of a central rounded nucleus with a single nucleolus, surrounded by a double membrane penetrated by a few pores (NP). The mitochondria are small and slightly expanded with short cristae, and there are many lipid granules (Li). Some X-cells show a dilation of the endoplasmic reticulum which may indicate the beginning of degenerative changes. Part of an endothelial cell (EC) of a capillary containing a red blood cell (RBC) can be seen. No connections were seen between endothelial cells and envelope cells.

FIGURES 6–7

FIG. 6. Electron micrograph of portions of X-cells (X) and a more granular envelope cell (E). The cytoplasm of the X-cells contains many vesicles of varying electron density. Some are electron transparent with a small polygonal dark body to one side (V_1), others are electron dense (V_2), and are sometimes closely associated with the cell membrane, indicating that they are pinocytotic vesicles. Smooth membranes are associated with the lipid granules (Li), and rough endoplasmic reticulum and ribosomes are also evident. There is an electron dense membrane (Me) external to the cell membrane of the X-cell, which cannot be seen around the envelope cell; FIG. 7. Electron micrograph of two X-cells (X) showing extensive invaginations (I) of the cell membrane and outer diffuse layer. There are many lipid granules (Li), dense polygonal granules in membrane-bound vesicles (V_1), and mitochondria (Mi) in the cytoplasm of these cells. Also shown are an envelope cell (E) and a degenerate X-cell (DX).

See page 1526 for figure captions 8–10.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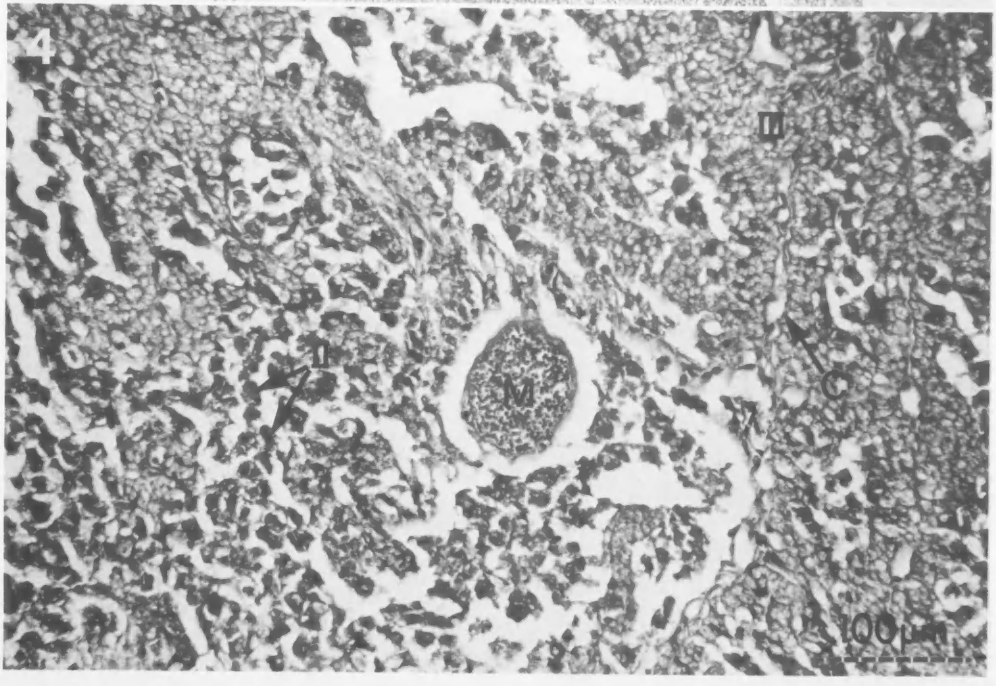
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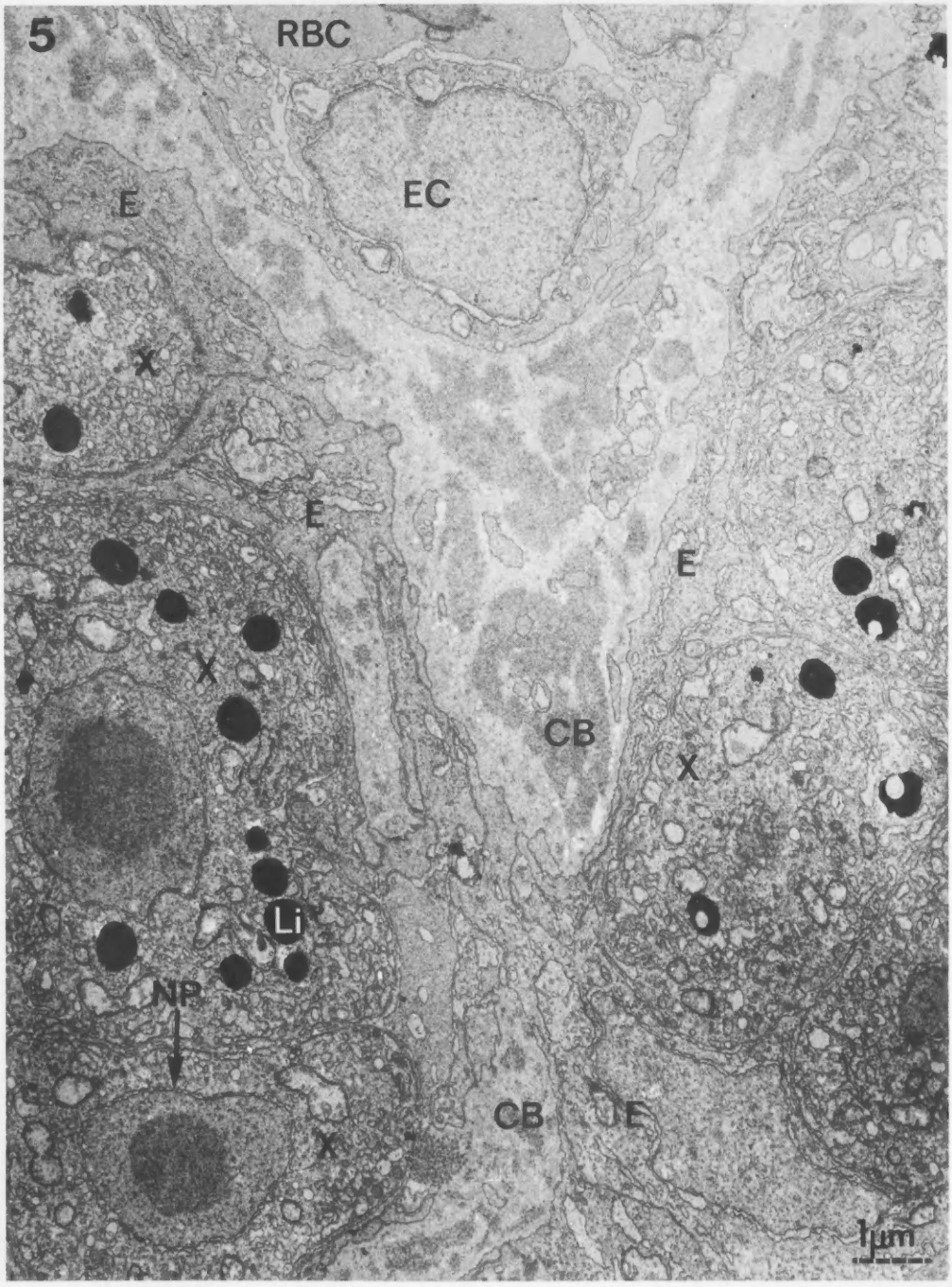
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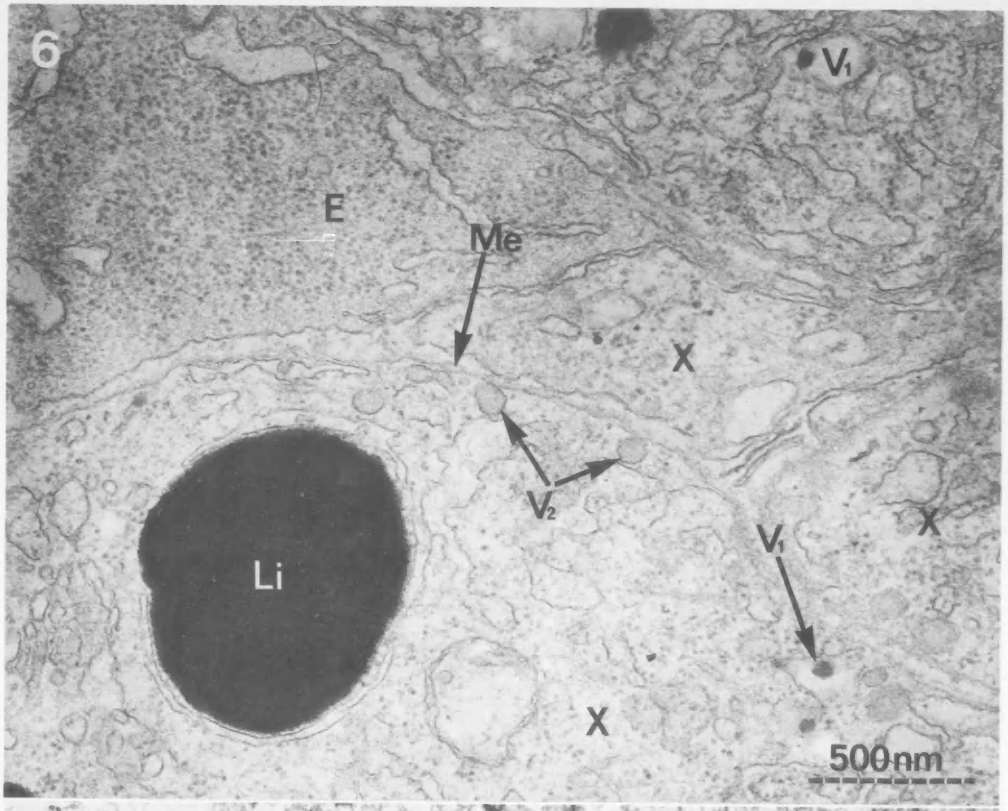
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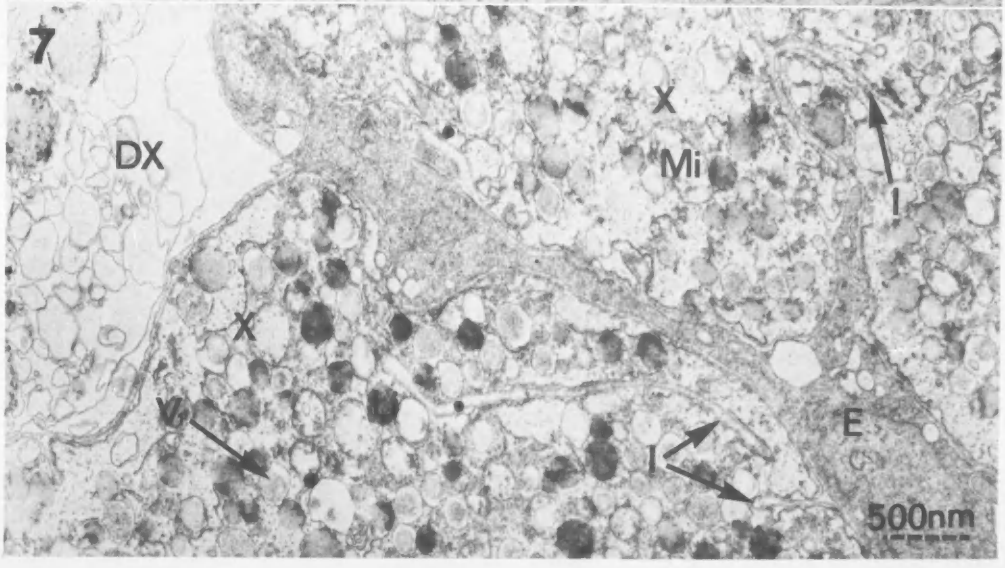
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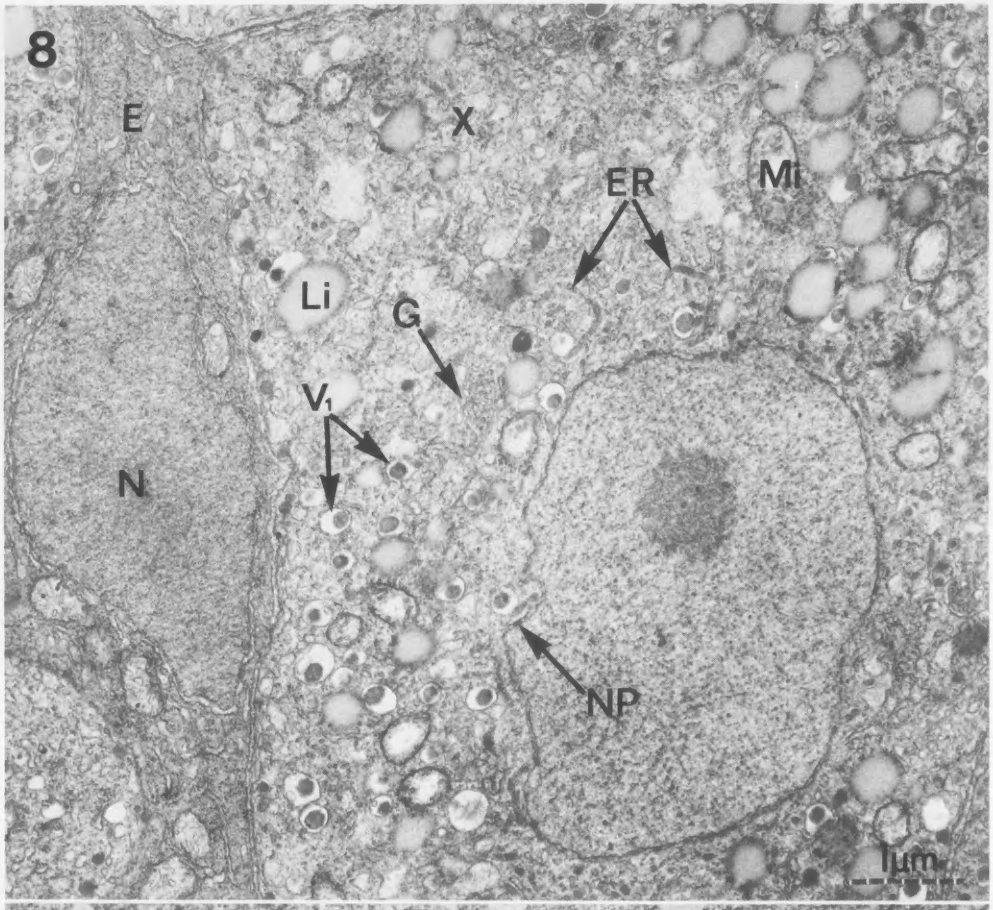
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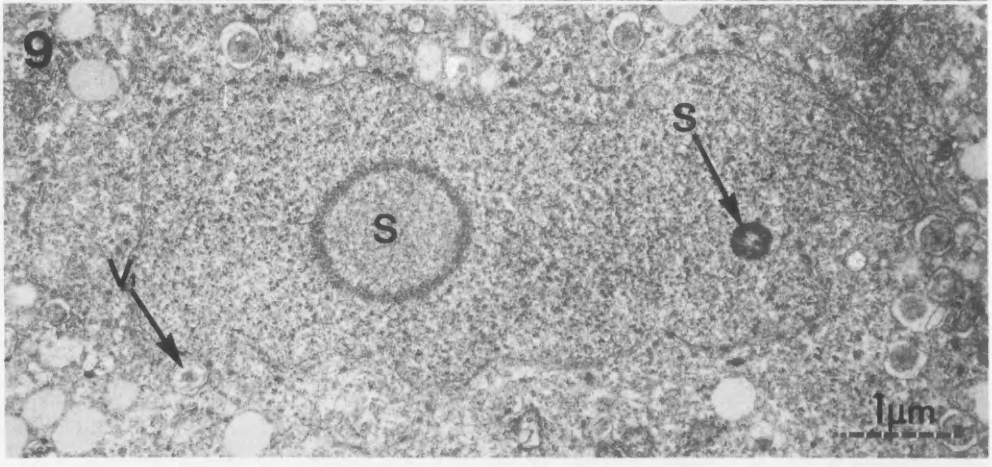
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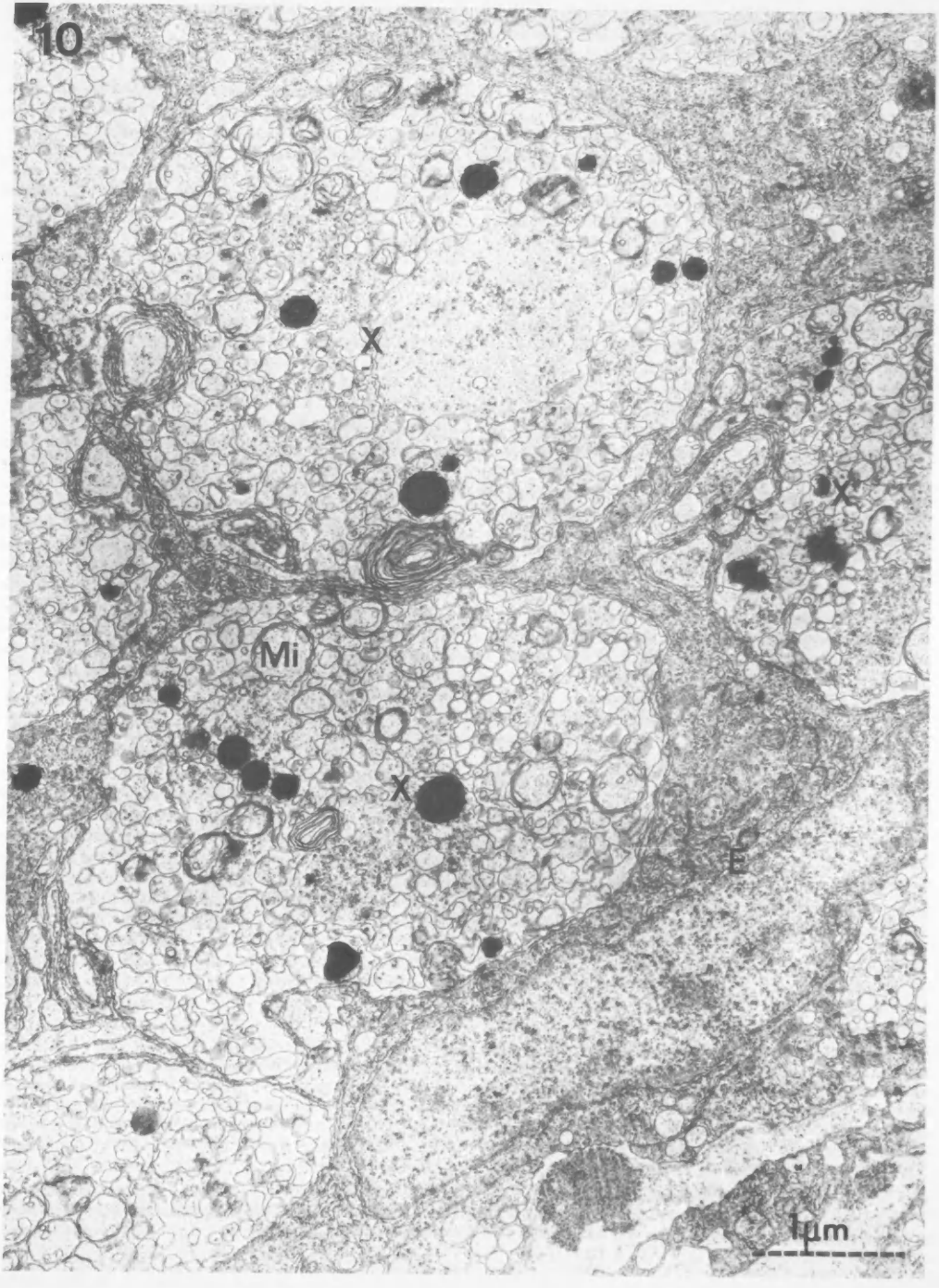
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Atlantic. Results are compared with findings of previous studies. The terminology used in describing the cell types found in the X-cell lesion follows that of Alpers et al. (1977).

Materials and Methods

Atlantic cod were collected by otter trawl in the southern Gulf of St. Lawrence, Nova Scotian Shelf and Bay of Fundy from 1974 to 1976. Fish were also obtained from inshore fishermen in the Halifax, N.S., area in October and November 1978, January, February, May, July, August, September, and November 1979, and November 1980. The number of fish in each Halifax sample was usually 50–100.

Histological examination by light microscopy was carried out on 22 pseudobranchs with X-cell lesions and 87 apparently normal pseudobranchs of live cod from the Halifax area. The external surface and internal organs of the fish with X-cell lesions were examined for abnormalities. The tissues were fixed in 10% neutral buffered formalin. Some material was prepared for frozen sectioning and staining with Oil Red 0 and Sudan Black B for fat, whereas most was dehydrated in an ethanol series and embedded in paraffin. Sections were cut at 7 μm and stained by the Harris' hematoxylin and eosin, P.A.S., Alcian blue and Fontana–Masson methods (Humason 1979). For electron microscopy, 1-mm cubes of tissue from the X-cell lesions of six fish and the pseudobranchs of two fish without lesions were fixed at 4°C in 4% formalin and 0.5% glutaraldehyde in 0.1 mol/L phosphate buffer, postfixed in 1% osmium tetroxide, dehydrated in an acetone series, and embedded in Taab resin (Marivac Co.). Thin sections were stained with uranyl acetate and lead citrate and examined using a Hitachi HS-9 electron microscope.

Some cod with and without X-cell lesions were held in the live holding facilities of the Halifax Laboratory for observation. Six cod with lesions were tagged and placed in a tank with 12 cod without lesions. Twelve cod without lesions were placed in an identical adjacent tank. These fish were kept under observation for 5 mo (Nov. 25, 1980 to Apr. 15, 1981), and any mortalities examined. Another cod with a bilateral lesion was placed in a tank with 2 cod without lesions for 2 mo (May 18, 1979 to July 18, 1979). The cod kept for 5 mo were anesthetized with MS222 and examined for developing X-cell lesions after 3 mo, then replaced in the tank. Both groups were anesthetized at the end of the observation period, and specimens were taken for histological examination.

Observations

Gross Appearance

The X-cell lesions were well defined, yellowish, lobulated masses found in one (unilateral) or both (bilateral) of the dorsal pre-esophageal depressions in the mouth of cod (Fig. 1 and 2). No X-cell lesions were found elsewhere in the body. Of 84 X-cell lesions examined, 79 (94%) were bilateral. These lesions were usually relatively small circular masses (1.5–2.0 cm in diameter) contained within the pre-esophageal depressions which are fairly deep and well-defined in Atlantic cod. Sometimes, however, the lesions formed larger circular or irregularly shaped masses which extended beyond the depressions and met on the medio-dorsal surface of the pharynx. X-cell lesions infrequently extended into the inner surface of the operculum and caused erosion of the opercular margin (Fig. 1), or extended dorso-posteriorly toward the head kidney. The pseudobranch was visible on the surface of the lesion except in one case where the pseudobranch was anterior to and not adjacent to the lesion (Fig. 2). X-cell lesions were firm to soft in texture and sometimes contained a liquified center. Right and left masses of bilateral X-cell lesions sometimes differed in size and consistency.

The X-cell lesions in cod held for observation usually remained unchanged in shape and size. Five cod with lesions and one without a lesion died of bacterial infection in the group held for 5 mo, and the lesion was often ulcerated. No new X-cell lesions developed in this group. The cod with lesions held for 2 mo remained unchanged in appearance, but one cod with no X-cell lesion held with it developed a large unilateral lesion, which did not show any clear connection with the pseudobranch, but extended posteriorly to the wall of the body cavity.

Histology

In all 87 apparently normal pseudobranchs examined histologically, there were no X-cells. Pseudobranchs lay within the pre-esophageal depressions and were surrounded by small amounts of connective tissue. Nine otherwise normal pseudobranchs contained cysts of microsporidians, probably *Loma morhua* (Morrison and Sprague, 1981) which were sometimes invaded by phagocytes and surrounded by an outer fibrous capsule. One contained a fungus, perhaps *Ichthyophonus*

Figures 8–9

Fig. 8. Electron micrograph of portion of unilateral X-cell lesion which developed in 2 mo in a cod kept in captivity. The X-cells (X) are large, and contain many mitochondria (Mi), V_1 vesicles and lipid droplets (Li). There is an extensive network of endoplasmic reticulum (ER), many free ribosomes, and a system of interconnected cisternae which may be the Golgi apparatus (G). The nucleus is irregular in shape, and the nuclear pores (NP) are filled with electron-dense material. The envelope cell (E) shows a typical elongated nucleus (N) and granular cytoplasm; Fig. 9. Electron micrograph of part of an X-cell from same lesion as Fig. 8. This cell was not surrounded by envelope cells. Two unusual structures (S), presumably of nucleolar derivation, are present in the nucleus. This was the only evidence we found of cell division. Some of the membrane-bound dense granules (V_1) have a dense core.

Fig. 10. Electron micrograph of degenerating X-cells (X). The nucleus has sparse chromatin, no nucleolus and a single nuclear membrane. The cytoplasm is heavily vacuolated. The mitochondria (Mi) are rounded off, the tubular nature of the endoplasmic reticulum can no longer be recognized, and myelin figures are present. The envelope cells (E) seem to be less degenerate.

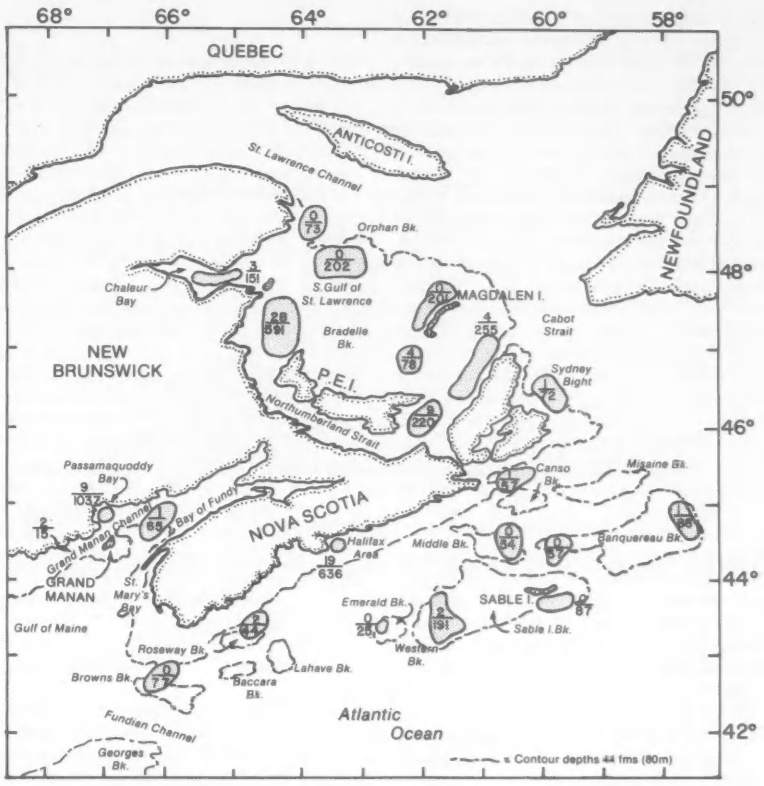

FIG. 11. Prevalence of X-cell lesions in Atlantic cod from the coast and continental shelf of eastern Canada.

hoferi Plehn and Mulsow. Small cysts whose contents could not be identified were present in some other pseudobranchs.

In the twenty-two fish with X-cell lesions, the mass of the lesion lay between the floor of the pre-esophageal depression and the pseudobranch, where there is normally little tissue. The pseudobranch was adherent to the pharyngeal epithelium and therefore never covered by the lesion (Fig. 3). The X-cell lesion was separated from the pharyngeal epithelium by connective tissue. Two X-cell lesions contained microsporidian cysts (Fig. 4). There was no host reaction around these cysts. The X-cells were P.A.S. and Alcian blue negative. The Fontana–Masson stain was generally negative, and the patchy positive staining is regarded as artefact. As reported in previous studies numerous granules in all X-cells stained with Oil Red 0 and Sudan Black B.

We found relatively few groups of Type I cells that did not show what appeared to be degenerative changes (Fig. 5). These usually occurred in the lesion near the pharyngeal epithelium. The envelope cells surrounding the X-cells were closely associated with groups of collagen fibrils and fibroblasts in the connective tissue septa in the lesion. The envelope cells and fibroblasts were similar in the elongate shape of the nucleus, the density of the cytoplasm and large mitochondria with well developed cristae. Some envelope cells had an extensive Golgi apparatus and rough endoplasmic reticulum like that of fibroblasts.

The X-cell cytoplasm contained small, rounded mitochondria with short cristae, free ribosomes, and smooth and rough endoplasmic reticulum (Fig. 6). Marginally placed dense bodies within vesicles were typical of X-cells. These bodies were usually polygonal in shape but varied in size in different X-cells (Fig. 6, 7, 8, and 9-V_1). Small, electron-dense vesicles were usually present in the peripheral cytoplasm and were sometimes closely associated with the cell membrane, indicating a pinocytotic origin (Fig. 6). Lipid droplets were always present, often associated with smooth membranes. There was always a somewhat diffuse coat outside the cell membrane, as described by other authors. A few X-cells had invaginations of the cell membrane and outer diffuse coat (Fig. 7-I). The part of the lesion that had spread towards the head kidney in the cod which developed a unilateral X-cell lesion in 2 mo was studied: some of the X-cells were enlarged and packed with well-developed organelles (Fig. 8). The nucleus was usually more irregular in shape than

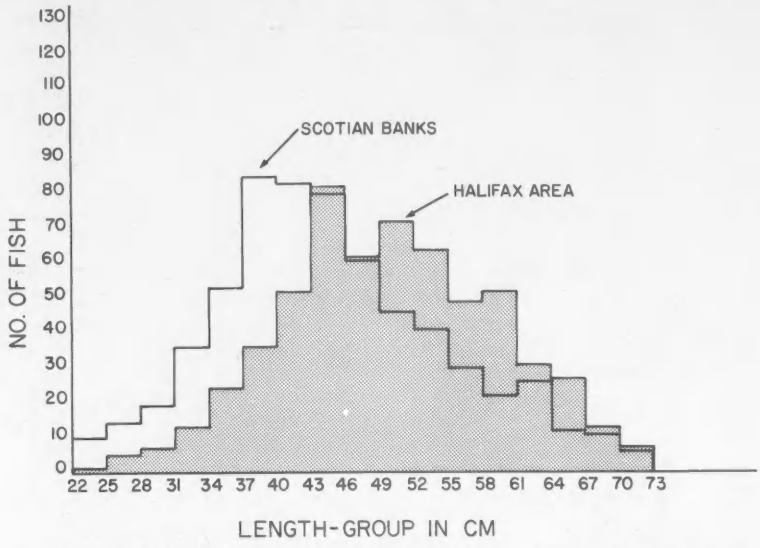

FIG. 12. Size distribution of cod caught from inshore Halifax area and offshore Nova Scotia banks.

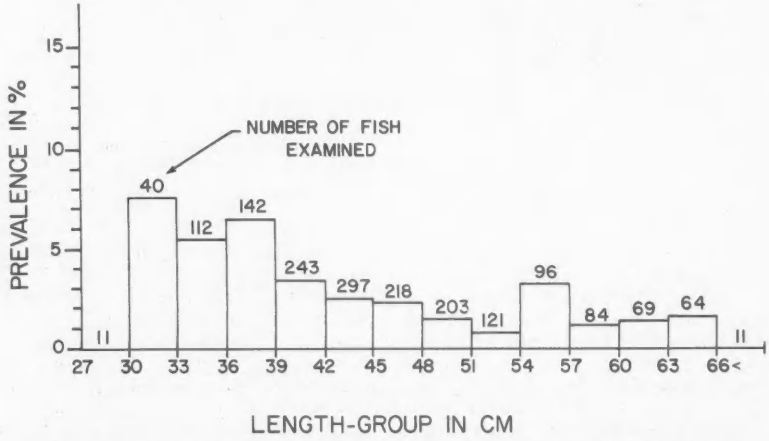

FIG. 13. Prevalence of X-cell lesions in different length-groups of Atlantic cod, caught in the southern Gulf of St. Lawrence.

that of most Type I X-cells, and the nucleolus often contained areas of reduced density. In one case two nucleoli of unusual shape were seen (Fig. 9).

Sometimes the arrangement of Type I, II and III X-cells was like that described by Alpers et al. (1977), but we often found that the X-cells bordering the perivascular sheaths still had a visible nucleus and nucleolus so probably corresponded to Type II cells, whereas large areas in the centre of the lesion were often filled with Type III X-cells in various stages of necrosis. Some areas of closely packed X-cells differing in cytoplasmic density, like those described by Lange and Johannessen (1977) were found, and the X-cells also varied considerably in number and size of lipid droplets. At the ultrastructural level we found that these variations were caused by different types of degeneration. Some degenerating X-cells developed large lipid droplets, whereas others underwent the changes shown in Fig. 10. Envelope cells showed fewer degenerative changes than X-cells.

EPIZOOTIOLOGY

Of 4256 Atlantic cod examined throughout the study area (Fig. 11), 86 (2.0%) had X-cell lesions. Prevalence was highest adjacent to land, e.g. near Halifax (3.0%, n = 636), Chaleur Bay (2.0%, n = 151), northwestern P.E.I. (4.7%, n = 591) and eastern P.E.I. (4.1%, n = 220), and lowest at the offshore Nova Scotian banks (0.9%, n = 660). Passamaquoddy Bay was an exception with a prevalence of 0.9% (n = 1,037). The fish from the Halifax area, which were caught at various times of year over a two year period, showed considerable variation in prevalence of X-cell lesions (1.5–6.1%), with no correlation with time of year. A comparison of fish size from an offshore area, the Scotian Banks, and an inshore area, around Halifax, showed only a slight difference (Fig. 12).

X-cell lesions were more prevalent in small cod and female cod. Gulf of St. Lawrence cod between 30 and 39 cm long were most frequently infected with a more or less gradual decline of prevalence in larger fish length-groups (Fig. 13). Since commercial trawls were used, few small fish were obtained as can be seen in this figure. The smallest fish sampled in this study was 16 cm long, and the smallest found with an X-cell lesion was 26 cm long. Of 71 fish with X-cell lesions categorized by sex, 44 (62%) were female. Of 57 cod categorized as to maturity, all were either immature or in a resting stage with the gonads relatively underdeveloped.

Discussion

While X-cell lesions of cod from the Canadian Atlantic are in general morphologically similar to those described by previous workers, several differences exist. In the present study, the pseudobranch was always found intact on the exposed surface of the lesion and never infiltrated by X-cells. Previous descriptions from the European Atlantic (Lange 1973) and Pacific cods (Alpers et al. 1977) indicated that only remnants of normal pseudobranch tissue were present surrounded by the X-cell lesion. The extent of lesion invasion also varies. X-cell lesions described by Alpers et al. (1977) varied in size but did not invade other tissues whereas those described by Lange and Johannessen (1977), and to a lesser extent the present study, infiltrated surrounding muscle tissue and the operculum. Lange and Johannessen (1977) described an isolated X-cell lesion on the nose of one cod with bilateral X-cell lesions and a temporal lesion unconnected with the pseudobranch. We also found X-cell lesions unconnected with the pseudobranch, which indicates that the lesion does not arise from pseudobranch tissue.

As found in previous studies, X-cell lesions were composed of X-cells and envelope cells (Alpers et al. 1977) separated into compartments by connective tissue septa containing blood vessels. The multinucleate stages of Alpers et al. (1977) were not observed. In this study we attempt to show features which we believe typify the normal X-cell. Variations from this morphology, such as those shown in this report and by Lange and Johannessen (1977) appear to be caused by degeneration. One specific feature is the vesicles containing marginally placed, normally polygonal dense bodies. Membrane bound dense bodies have been described in gadoids and pleuronectids (Alpers et al. 1977). These authors suggest that the granules are similar to those in APUD cells, but we found that the position and shape of the dense granules shown in X-cells in our micrographs were not the same. The polygonal shape could indicate that the dense bodies are viral in nature, but their variation in size makes it more likely that they are a specific organelle or secretory product of the X-cells. We cannot comment on the composition of these granules, since we obtained negative results with our staining methods. We describe some X-cells which seem to be in a very active state, with nucleolar changes unlike those of host cells. Unidentified "amoeboid" cells have been described in the dab, *Limanda limanda* (Watermann 1982). These have vesicles with marginal polygonal granules, and invaginations like those found in one group of X-cells in this study. These features, along with the prominent nucleolus, mitochondria with short cristae and diffuse coat outside the cell membrane make it likely that these "amoeboid" cells are X-cells. It seems that X-cells are widely distributed protozoan parasites which do not necessarily form a tumor-like lesion. The pseudobranch region of cod is shown in this study to be a common site for parasitic infection.

No invasion of X-cells by phagocytes was seen, although invasion of microsporidian cysts and other parasites by host phagocytes followed by formation of a fibrous capsule was common in the pseudobranch and the connective tissue around it. The granulomas reported by Alpers et al. (1977) may be of this type. Possibly the envelope cells, which have features in common with fibroblasts, are a form of host reaction. Their action of surrounding the X-cells could be related to the degeneration of most of the X-cells in the lesion. The outer diffuse coat of the X-cell may prevent recognition as an antigen by the host, so that phagocytes do not accumulate.

The prevalence of X-cell lesions in the Canadian Atlantic (0.9–4.7%) is similar to Atlantic cod from the German Bight (2.1%) (Watermann and Dethlefsen 1980) but lower than the prevalence of these lesions in Pacific cod from British Columbia (2.2–11.4%) (Stich et al. 1976) and the Bering Sea (8.7%) (McCain et al. 1979). However, as in the Pacific cod, X-cell lesions described here are more common in some areas than others, and further sampling in the Canadian Atlantic may find more intense foci of prevalence of X-cell lesions. Possibly prevalence of X-cell lesions could be used as a population tag, since the lesions are easily identified and, with care, fish could be examined and replaced alive in the ocean. The increased prevalence of X-cell lesions inshore compared to offshore could be associated with the presence of an intermediate host, or with more variable conditions in some inshore areas, which would expose the animals to extra stress and encourage the spread of parasites. There seems to be no correlation with areas that would be expected to have high levels of pollution.

Small fish are more often afflicted than larger fish (Stich et al. 1976, present study); but since there is no large difference in size of inshore and offshore fish, one cannot explain the increased prevalence of X-cell lesions from inshore fish on the basis of an increased number of small fish in inshore populations. The lack of X-cell lesions in fish below 26 cm is probably not significant since so few fish below this size were

sampled. In larger fish the lesions must either regress or cause mortality. It appears that in the right conditions the X-cell lesion can develop very rapidly, since no early stages in lesion development were found, and a lesion developed very rapidly in one case. This potentially rapid development of X-cell lesions and the large size of some lesions described indicate that they could place appreciable stress on the fish. This may explain the retardation of gonad development, and the high mortality from bacterial infection of fish with X-cell lesions held in captivity. Both the possibility of a high mortality among juveniles and lower fertility in cod with X-cell lesions need further investigation, since as many as 100% of small Pacific cod in some areas had the lesion (Stich et al. 1976) and, in the present study, a fair proportion of young fish had lesions in some populations (e.g. 12.5% of cod 30–39 cm in length in the group from northwestern P.E.I.). This could have an appreciable effect on the inshore fishery in some areas.

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NOTES

Effects of Upwelling on Local Abundance and Distribution of Larval Alewife (*Alosa pseudoharengus*) in Eastern Lake Michigan[1]

GEORGE R. HEUFELDER, DAVID J. JUDE, AND FRANK J. TESAR

Great Lakes Research Division, Institute of Science and Technology, University of Michigan, Ann Arbor, MI 48109, USA

HEUFELDER, G. R., D. J. JUDE, AND F. J. TESAR. 1982. Effects of upwelling on local abundance and distribution of larval alewife (*Alosa pseudoharengus*) in eastern Lake Michigan. Can. J. Fish. Aquat. Sci. 39: 1531–1537.

Intrusion of cold (usually <10°C), hypolimnetic water into the Lake Michigan nearshore zone (≤15 m) substantially changed local abundance and distribution of larval alewife (*Alosa pseudoharengus*) during the summers of 1977–79. During upwelling, larval fish densities were reduced to below 1000 larvae/1000 m^3; when no upwelling occurred densities commonly exceeded 5000 larvae/1000 m^3. Widespread distribution to depths of at least 15 m was found in the absence of upwelling, while during upwelling larvae were more concentrated in water ≤6 m deep. Additionally, at depths >3 m during upwelling, alewife larvae were most abundant in bottom strata, a trend not observed in the absence of upwelling. Postulated mechanisms for reduced larval alewife abundance in inshore areas during upwelling include mortality of larvae due to thermal shock, and offshore or alongshore movement, either actively by larvae and potential spawning adults, or passively by larvae.

Key words: *Alosa pseudoharengus* larvae, distribution, abundance, Lake Michigan, upwelling

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Pendant les étés de 1977–79, l'intrusion d'eau hypolimnétique froide (ordinairement <10°C) dans la zone côtière (≤15 m) du lac Michigan produisit un important changement d'abondance locale et de distribution des larves de gaspareau (*Alosa pseudoharengus*). En périodes de remontées d'eaux profondes, la densité des larves diminue à moins de 1 000 larves/1 000 m^3; en l'absence de remontées, la densité dépasse communément 5 000 larves/1 000 m^3. Quand il n'y a pas de remontée d'eaux profondes, on trouve les larves largement répandues à des profondeurs d'au moins 15 m, alors qu'en périodes de remontées, les larves sont concentrées dans des eaux ≤6 m de profondeur. En outre, à des profondeurs de >3 m en périodes de remontées, les larves de gaspareau sont plus abondantes dans les couches de fond, une tendance qui n'apparaît pas en l'absence de remontée. Parmi les mécanismes que l'on suppose responsables de la diminution d'abondance des larves de gaspareau dans les régions côtières en périodes de remontées d'eaux profondes, on note la mortalité des larves à la suite d'un choc thermique et un mouvement vers le large ou le long du rivage, soit activement par les larves et des adultes potentiellement reproducteurs, ou passivement par les larves.

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WIND-INDUCED upwelling commonly occurs in Lake Michigan throughout summer and autumn, particularly from July through November (Mortimer 1975; Jude et al. 1979b). The effect of displacing warm inshore water with cold hypolimnetic water on adult fish distributions is often considerable. Jude et al. (1979b) observed that during summer the inshore movement by juveniles and adults of stenothermal species such as lake trout (*Salvelinus namaycush*), rainbow smelt (*Osmerus mordax*), and bloater (*Coregonus hoyi*)

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coincides with the inshore movement of the thermocline. Movements of warmwater species such as alewife (*Alosa pseudoharengus*), spottail shiner (*Notropis hudsonius*), and yellow perch (*Perca flavescens*) are not as prominent, but these taxa do appear to concentrate inshore of the thermocline, demonstrating their preference for warmer inshore water (Jude et al. 1979b). Although responses of other species to shifts in the thermocline in the Great Lakes have been documented, these observations were also of juveniles and adults (Emery 1970). Response of alewife juveniles and adults to temperature regimes was comprehensively studied by Brandt (1980). Our study documents the effect of upwelling on local abundance and distribution of larval alewife in eastern Lake Michigan.

Materials and methods — The study area was located in eastern Lake Michigan approximately 3.1 km south of Port Sheldon, Michigan. Day and night sampling was performed twice per month from June to August 1978–80 and June and July 1977 at seven stations. One day and one night sample were taken in April and May 1978–80, August 1977, and September 1977–80. Samples were collected at depths ranging from 1 m (beach) to 15 m at various depth strata including the bottom.

Depth strata (except bottom) were sampled with a 0.5-m diameter, nylon plankton net of 363-μm mesh. The bottom stratum was sampled with the same size and mesh net mounted on a benthic sled with a rectangular frame (Yocum and Tesar 1980). For surface tows at the 1-m contour, two nets were hand towed simultaneously for a distance of approximately 61 m. All other samples consisted of single, horizontal, 5-min tows taken from a boat at an average speed of 5 km/h. A flowmeter mounted centrally in the opening of each gear measured volume of water filtered. Samples were preserved in 10% buffered formaldehyde. Alewife larvae sorted from the samples were measured to the nearest 0.5 mm total length. An arbitrary length limit of 25.4 mm was used to define larval alewife for the purpose of our analyses.

Results — Larval alewife were most abundant during July and August and hence the effect of upwelling on their distribution and abundance was most evident during these months. Comparing larval alewife abundance in 1979, when upwelling occurred during both July sampling periods, with abundance in 1980, when no upwelling occurred during the July and August sampling periods, provided data to best elucidate the effect of upwelling on larval alewife. Data from 1977 and 1978 are presented in a partial and auxiliary manner here to support conclusions; however, these data are presented in their entirety in Jude et al. (1981). Meteorological data recorded during collection times (Jude et al. 1980) show that deflections in the 1979 summertime warming trend (Fig. 1) were attributable to upwelling rather than internal waves (i.e. seiches).

Upwelling events appear to have caused a decrease in local abundance of alewife larvae. Peak densities of alewife larvae during both July periods of 1979, coincident with upwelling, were generally less than 1000 larvae/1000 m^3 and larvae were absent from many depth strata (Fig. 2). Similarly, in late July 1977 when upwelling depressed water temperatures to <10°C at depths >3 m, alewife larvae were absent from many depth strata, and peak densities did not exceed 800 larvae/1000 m^3 at depths >3 m (Jude et al. 1978). Conversely, during 1980 when a warming trend continued uninterrupted through both July sampling periods, densities of alewife larvae at most depths exceeded 1000 larvae/1000 m^3 and densities as high as 5000 larvae/1000 m^3 were common (Fig. 2). During 1977 and 1978, the early July sampling periods coincided with water temperatures generally exceeding 16°C and, as in July 1980, densities at most depth contours exceeded 1000 larvae/1000 m^3. While upwelling did not occur during late July sampling in 1978, densities of alewife larvae generally did not exceed 1000 larvae/1000 m^3. Examination of water temperatures recorded daily at the Grand Rapids water intake (10.7 km north of the study area) indicated that upwelling had occurred between sampling dates in July 1978 but its effect on larval alewife densities was only beginning to diminish by late July.

The distribution of larval alewife was also affected by upwelling. During 1977 and 1978 when no upwelling occurred during early July sampling, the distribution of alewife larvae was similar and comparable with both periods in July 1980 when larvae were abundant in almost all strata from shore to at least the 15-m contour (Fig. 2). During upwelling, however, the distribution of alewife larvae changed and greatest abundance occurred from shore to only the 6-m contour, e.g. during July 1979 (Fig. 2). Additionally, during upwelling alewife larvae were generally more abundant in the bottom stratum at depth contours >3 m, and their presence in overlying strata was only sporadic (Fig. 2). Data from late July 1978, when sampling followed upwelling by approximately 1 wk, showed that larvae were widespread throughout the study area, which was similar to the distribution pattern observed during times of no upwelling (Jude et al. 1979a). Densities of larvae, however, were much lower, generally <500 larvae/1000 m^3, than were observed during periods of no upwelling.

During 1979, a year of frequent and prolonged upwelling, there was a substantial difference in the size composition of alewife larvae in late July compared with other years sampled. During 1977, 1978, and 1980 at least 50% of the larvae captured in late July were larger than 5.0 mm, suggesting that the early July hatch of those years was well represented in the late July catch (Fig. 3). However, in late July 1979, only 1% of the alewife larvae caught exceeded 5.0 mm and thus the early July hatch of that year was underrepresented in the late July catch compared with other years sampled. These data suggest that frequent and prolonged upwelling throughout July 1979 may have either resulted in mortality for many larvae that hatched just prior to or during upwelling, or caused greater and more continuous displacement of larvae from the inshore zone than had occurred in July of other years sampled.

Upwelling events prolonged the period of occurrence of newly hatched alewife larvae in direct proportion to the frequency and duration of upwelling during the spawning season. During 1980, when the spring-to-summer warming trend in the study area went essentially uninterrupted, there was a clearly defined hatching peak in early July which showed a slight tapering off in late July and a substantial tapering off in early and late August (Fig. 2, 3). In contrast, the 1979 spawning season was interrupted by extensive upwelling which kept

the recruitment of newly hatched larvae at a low level throughout July, thereby causing a hatching peak in August which may have extended into September. This is supported by length-frequency data from September 1979 which differed substantially from all other years. Many larvae captured in September 1979 (over 50%) were less than 15 mm, indicating that many were hatched in September (Fig. 3). September catches in 1977, 1978, and 1980 yielded no larvae smaller than 15 mm, indicating that little or no reproduction occurred in September of those years, despite water temperatures conducive to spawning. In 1977 and 1978 a major hatching peak in early July was interrupted by upwelling later in July; a resumption of spawning occurred in early August. In both these years, however, recruitment of newly hatched larvae terminated by mid-August.

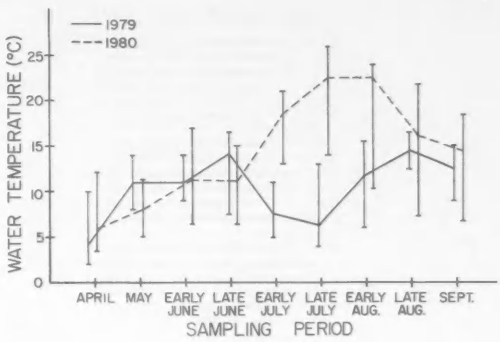

FIG. 1. Mean (n = 60, all depth strata) water temperatures and ranges (vertical lines) measured in eastern Lake Michigan during the 1979 and 1980 sampling periods.

Discussion — Mechanisms by which upwelling can affect alewife larvae abundance are varied and complex. The possibility that lowered water temperatures have an inhibiting effect on potential spawning adults in the area, which would ultimately reduce recruitment of newly hatched larvae, is supported by the observation that many alewife adults moved from the inshore zone (depths 15 m or less) during times of upwelling in 1977 and 1979 to either offshore areas or areas not affected by upwelling (Jude et al. 1978, 1980). Emery (1970) observed alewife adults moving upward in the water column and staying in warm surface water when the thermocline moved shoreward and brought hypolimnetic water into 2–11 m in Georgian Bay, Lake Huron. Larval alewife densities may also be depressed during upwelling due to the active or passive movement of larvae offshore or alongshore with the warmwater mass during initial upwelling formation. Inability of newly hatched alewife larvae to swim against water currents, such as offshore currents produced during upwelling formation, has been suggested by Jude et al. (1978, 1979a, 1980, 1981). These investigators hypothesized that alewife larvae have a passive stage, similar to the closely related Atlantic herring *Clupea harengus* (Graham et al. 1972), during which net horizontal movement is in the direction of prevailing water currents. Transport of marine clupeoid larvae in offshore-moving water masses during upwelling of Spanish Sahara was documented by Blackburn and Nellen (1976). Decreased abundance of alewife larvae during upwelling may also be caused in part by direct mortality of larvae as documented by laboratory studies of Edsall (1970). He found that alewife eggs cultured at temperatures <10°C resulted in larvae which failed to develop a functional jaw. Since this and other deformities relating to locomotion increase with decreased water temperature, it is possible that eggs spawned and larvae hatched just prior to or during upwelling would experience higher mortality than those spawned at warmer temperatures. In the case of larvae which lacked a functional jaw, we would expect survival only until the time of endogenous energy exhaustion. This we believe may explain in part the lack of larvae exceeding 5.0 mm in late July 1979.

Reasons for the more nearshore distribution (primarily ≤6 m) of alewife larvae during upwelling remain unclear. During upwelling there is usually an extreme nearshore area (≤1.5 m) where water temperatures (Jude et al. 1981) marginally conducive to alewife spawning exist, and hence limited alewife spawning could have occurred there, accounting for the newly hatched larvae observed in the nearshore zone. Larger larvae captured in this zone during upwelling may be exhibiting a preference for the warmest water available locally. At those times during upwelling when all sizes of alewife larvae were captured at depths >3 m, the higher abundance of larvae in bottom strata samples may have been related to decreased swimming activity and decreased response to external stimuli (such as our sampling gear) associated with lowered water temperatures as has been reported to occur in adults (Colby 1973). At water temperatures quite common during upwelling events in our area (4.5–6.7°C), Colby additionally observed that adults showed reduced feeding and schooling activity.

The correlation of increased upwelling frequency with prolonged recruitment of newly hatched larvae suggests that upwelling events in our study area may play an important role in apportioning the reproductive effort of alewife adults over the spawning season. Implications of prolonging the spawning period are unclear. In the extreme case, as in 1979 when a portion of the reproductive effort was delayed until late August and September, it is possible that higher mortality of larvae might result in that year compared with years in which the reproductive effort was more confined to June–early August. Appropriate year-class strength data to support this hypothesis are, however, not available.

The extent to which upwelling events ultimately regulate the larval alewife population and hence the juvenile and adult alewife population in Lake Michigan is obscured by two main factors: mobility of juveniles and adults and the lack of spatially defined populations. In addition, upwelling on the eastern side of the lake can be accompanied by downwelling on the western side. Downwelling may stimulate increased spawning and hatching success in the western portion of the lake by providing prolonged periods of warm water inshore. Production lost due to an upwelling on the eastern shore would therefore be to some extent mitigated by increased production on the western shore, and eventually be obscured

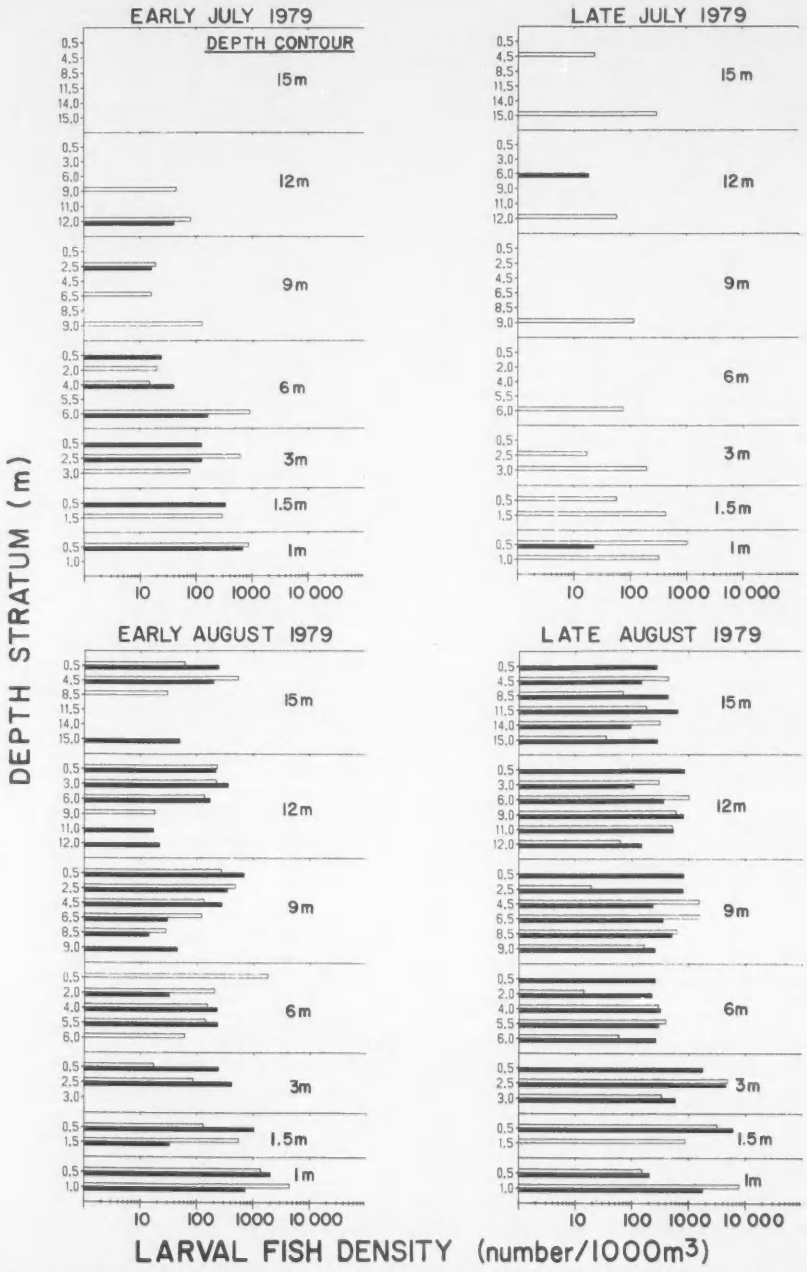

FIG. 2. Densities of alewife larvae collected in eastern Lake Michigan during July and August, 1979 and 1980. Solid bars = night, open bars = day. Upwelling occurred during early and late July 1979.

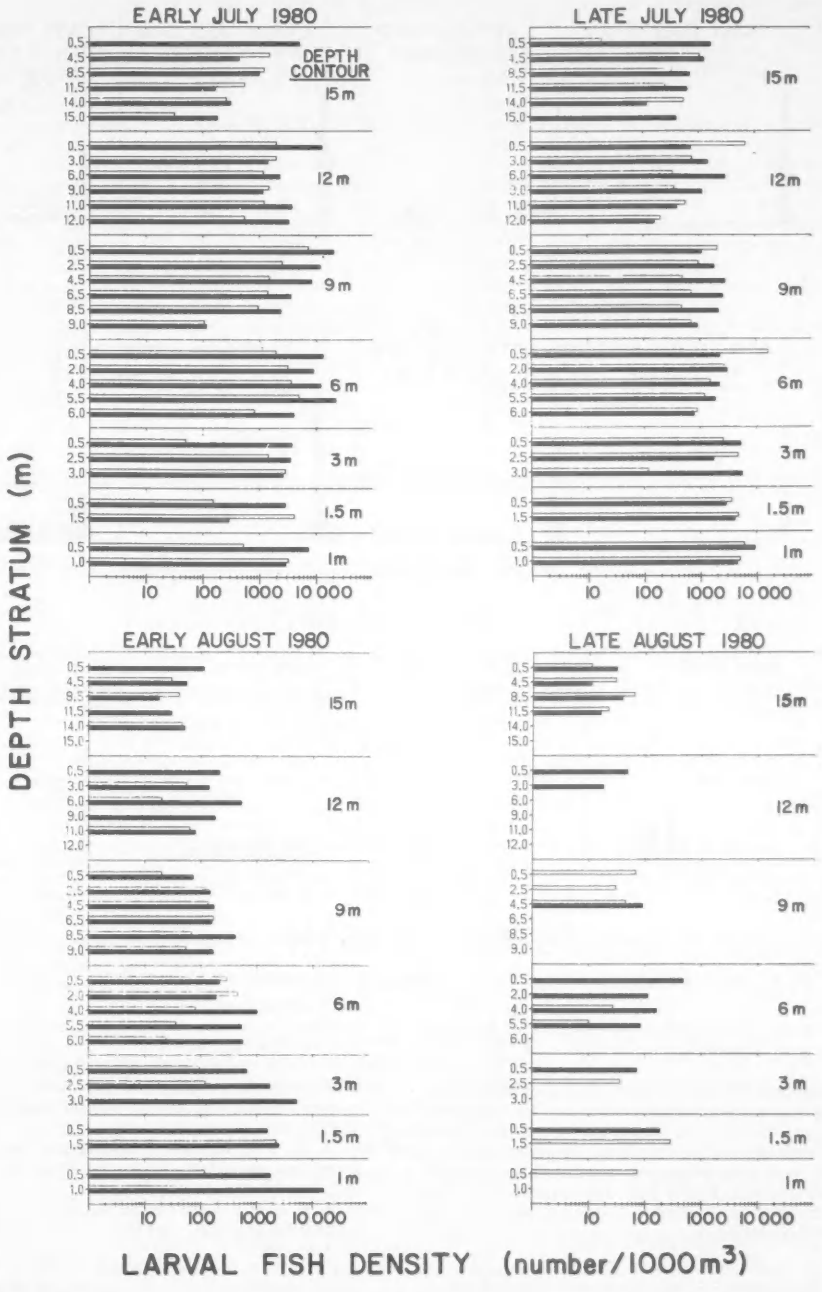

FIG. 2. (*Concluded.*)

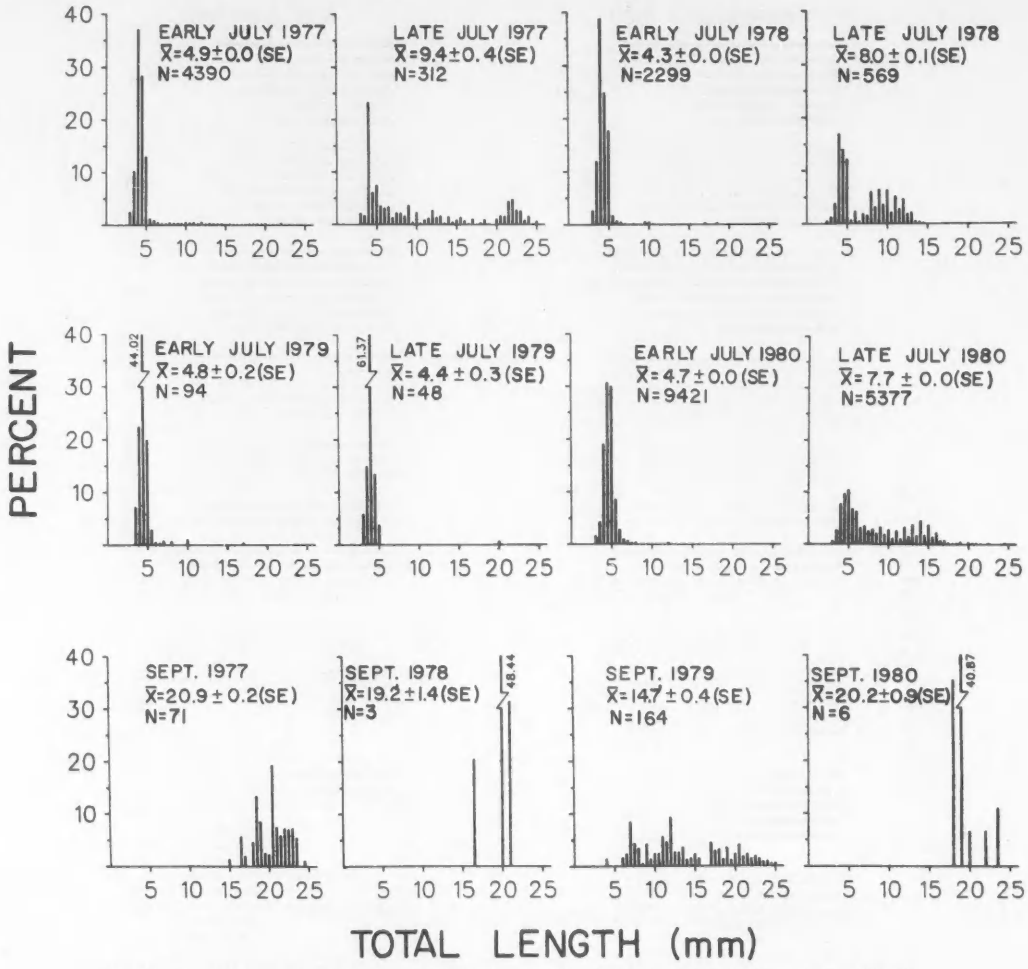

FIG. 3. Length–frequency distributions of alewife larvae collected in eastern Lake Michigan during 1977–80.

by the free exchange of juveniles and adults which probably eventually occurs between the two areas.

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Predation by Medusae on Pacific Herring (*Clupea harengus pallasi*) Larvae

MARY NEEDLER ARAI

Department of Biology, University of Calgary, Calgary, Alta. T2N 1N4

AND DOUGLAS E. HAY

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

ARAI, M. N., AND D. E. HAY. 1982. Predation by medusae on Pacific herring (*Clupea harengus pallasi*) larvae. Can. J. Fish. Aquat. Sci. 39: 1537–1540.

In laboratory tests young Pacific herring (*Clupea harengus pallasi*) larvae were eaten by several species of hydromedusae common in coastal waters off British Columbia, including the previously controversial *Sarsia tubulosa* and by the scyphomedusa *Aurelia aurita*. Field collections and observations confirmed that the distributions of medusae and larvae overlap and that some medusae feed on herring larvae in nature. In coastal waters and bays of British Columbia, the hydromedusae *Sarsia tubulosa* or *Aequorea victoria* may be most abundant during the time of peak herring larvae abundance.

Key words: herring, larvae, *Clupea*, *Sarsia*, *Aequorea*, predation, medusae

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Dans des essais en laboratoire, les jeunes larves de hareng (*Clupea harengus palasi*) ont été dévorées par plusieurs espèces d'hydroméduses communes des eaux côtières de la Colombie-Britannique, y compris *Sarsia tubulosa*, jadis controversée, et par la scyphoméduse *Aurelia aurita*. Des collectes et observations sur le terrain confirment que la distribution des méduses et des larves chevauchent et que certaines méduses se nourrissent de larves de hareng dans la nature. Dans les eaux côtières et les baies de la Colombie-Britannique, il se peut que les hydroméduses *Sarsia tubulosa* ou *Aequorea victoria* aient leur maximum d'abondance en même temps que les larves de hareng.

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ALTHOUGH medusae have been mentioned as possible predators of herring larvae in coastal waters off British Columbia (Stevenson 1962), no detailed studies have been made. Literature on medusae predation in other regions is very sparse and includes conflicting data. The hydromedusae *Phialidium hemisphaericum*, *Sarsia tubulosa*, *Rathkea octopunctata*, and *Bougainvillia superciliaris* and the scyphozoan *Aurelia aurita* have been observed eating herring larvae in the laboratory or in the field (Lebour 1922, 1923; Gudger 1934; Sveshnikov 1963; Fraser 1969; Möller 1980). The latter four species are present in British Columbia waters (Arai and Brinckmann-Voss 1980), however, other species common in the NE Pacific, such as *Aequorea victoria* and *Eutonina indicans*, have not been examined.

There is also controversy with reference to predation by *Sarsia*. Sveshnikov (1963) stated that *Sarsia tubulosa* actively hunt herring larvae and in the White Sea predation by this species may remove up to 10% of the herring larvae daily. However, Lebour (1923) did not find *Sarsia tubulosa* eating fish larvae even when confined together in a jar. Fraser (1969) found that closely related *Sarsia princeps* ate fish larvae only if they were deliberately given by the investigator and would otherwise lose fish touched by the tentacles during active movement.

The present note reports research investigating whether several species of medusae resident in British Columbia waters will eat herring larvae under laboratory conditions. Feeding by *Sarsia tubulosa* and *Aequorea victoria* was also directly observed in the field. The numbers of these medusae present in two bays bordering the Strait of Georgia during the period of maximum abundance of herring larvae was examined.

Materials and methods — Laboratory experiments — Medusae were dipped from Departure Bay or Ladysmith Harbor using glass containers. They were held in Departure Bay water at 10°C for at least 16–24 h prior to testing. Pacific herring, *Clupea harengus pallasi*, larvae were obtained from eggs fertilized and incubated in the laboratory and maintained at 10°C. They were tested both at the yolk-sac stage and within 2 d thereafter (both stages approximately 10–11 mm in length).

Duplicate experiments were conducted by placing five possible predators (medusae) and five potential prey (herring) in fresh seawater in 3.6-L glass jars maintained at 10°C. The number of prey eaten after 24 h were noted.

Field collections — During March and April, 1979, daily tows (Monday to Friday) were made in Departure Bay in the vicinity of the Pacific Biological Station. A 0.25 m^2 score net with 1 mm mesh openings was towed slowly for approximately 350 m at a depth of 1 m. The results of the five tows made each week were summed.

Tows were made during March and April of 1981 at three stations on each of three transects in southern Baynes Sound (see Fig. 1). Paired bongo nets (one of 350 μm and one of 500 μm mesh) were towed obliquely from 20 m depth to the surface. The specimens from the two nets were summed to give a filtered volume per haul of approximately 32 m^3. Horizontal tows were not made in Baynes Sound but horizontal tows in neighboring Lambert Channel on March 27 showed that herring larvae were concentrated in the upper 5 m. In Baynes Sound *Aequorea* and herring larvae were visually observed to be abundant in surface waters (upper 1–2 m).

All collected specimens were fixed immediately in 10% formalin in sea water.

Observations of medusae feeding on herring larvae were made from a boat in Baynes Sound and from the wharf at the Pacific Biological Station. The latter included observations made in the evening under the illumination of an incandescent bulb suspended from the edge of the wharf.

Results — Laboratory experiments — Herring larvae are eaten in the laboratory by *Bougainvillia multitentaculata*, *Sarsia tubulosa*, *Aequorea victoria*, *Eutonina indicans*, and *Aurelia aurita*, and to a lesser extent by *Stomatoca atra* and *Phialidium gregarium* (Table 1). Lack of predation by *Obelia* spp. and *Proboscidactyla flavicirrata* allowed complete survival in these tests to serve as a control for herring mortality. *Aurelia aurita* ephyrae were also tested but have not been included in the table due to a tendency for the ephyrae to release dead larvae previously swallowed (which causes very variable results). This tendency was not found in 8–18 mm *Aurelia*.

Field collections — The question arises whether the species that eat herring in the laboratory are in fact predators under field conditions. Evidence collected incidental to other investigations of herring larvae indicate that at least *Sarsia tubulosa* and *Aequorea victoria* are natural predators. We have seen both species eating herring larvae when the larvae have been attracted to a night light, and have collected both species with larvae in their stomachs. However, although both have been shown to be present in significant numbers at the same time as herring larvae are present in bays neighboring the Strait of Georgia, the numbers are very variable as indicated in the following examples.

In Departure Bay in 1979, herring larvae were present in large numbers during the last week of March and the first 2 weeks of April (Fig. 2). The most abundant genus of medusae during the same period was *Sarsia*, mostly *Sarsia tubulosa* (Fig. 2). Smaller numbers of *Rathkea octopunctata*, *Tiaropsis multicirrata* and *Eutonina indicans* were also collected. In contrast to the following data for Baynes Sound, *Aequorea victoria* was present only later in the season.

In Baynes Sound herring larvae reached a peak abundance in late March of 1981 and then declined through the first 2 weeks of April (Fig. 3). Although the volume filtered was only 32 m^3/haul so variability in numbers of medusae per haul was high, *Aequorea victoria* was clearly shown to be present in significant numbers over the same period. Even at the peak of the herring abundance the ratio of *Aequorea* to larvae was approximately 1:625. *Aequorea* counted were over 2 cm in diameter. Only occasional smaller *Aequorea* and *Sarsia* sp. were observed. In contrast, medusae were rare in neighboring Lambert Sound on March 27, 1981.

Discussion — Our laboratory work shows that herring larvae are eaten by several species of medusae, including five species not previously examined, when confined in aquaria.

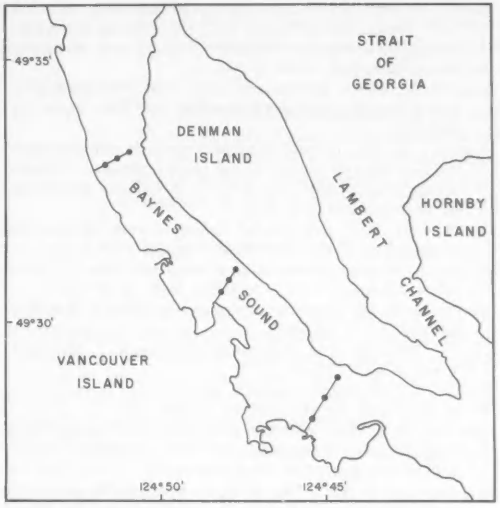

FIG. 1. Location of collecting stations in Baynes Sound, 1981.

TABLE 1. Predation by medusae on Pacific herring (*Clupea harengus pallasi*), number eaten per 10 prey tested.

Medusae	*Clupea harengus* larvae	
	yolk sac	post yolk sac
Anthomedusae		
Bougainvillia multitentaculata	10	10
Sarsia tubulosa adults	10	10
Stomotoca atra >10 mm	not tested	2
Leptomedusae		
Aequorea victoria 8–20 mm	10	8
20–40 mm	10	10
Eutonina indicans >15 mm	10	10
Obelia spp.	0	not tested
Phialidium gregarium >8 mm	6	6
Limnomedusae		
Proboscidactyla flavicirrata 4–7 mm	0	0
Scyphomedusae		
Aurelia aurita 8–18 mm	not tested	10

All genera previously implicated by other authors (see introduction) are confirmed except *Rathkea*. *Rathkea octopunctata* has been shown by Lebour (1923) and Sveshnikov (1963) to eat herring larvae under similar conditions. However, it is one of the earliest species in Departure Bay and was not available during our laboratory experimental period. With reference to the controversy over *Sarsia*, *Sarsia tubulosa* actively caught herring, as stated by Sveshnikov (1963). We did not observe any loss during active movement as stated by Fraser (1969) for *Sarsia princeps*.

The field observations in Departure Bay and Baynes Sound show that medusae are present in bays at the same time as herring larvae. The differences between the two examples indicate, however, that the particular species and hence the rate of predation may be variable. For example, *Aequorea victoria* is present in Baynes Sound while herring larvae are abundant but is only present later in the season in Departure Bay, conversely *Sarsia tubulosa* is abundant in Departure Bay. Although *Aurelia aurita* is known to be an important predator of herring larvae in Kiel Fjord, Baltic Sea (Möller 1980), it has been found in significant numbers in British

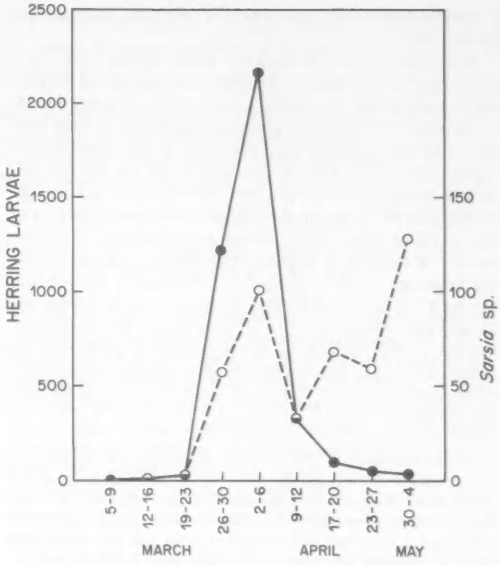

FIG. 2. Herring larvae (closed circles) and *Sarsia* sp. (open circles) medusae over 4 mm high in Departure Bay, spring 1979; numbers in five tows per week summed.

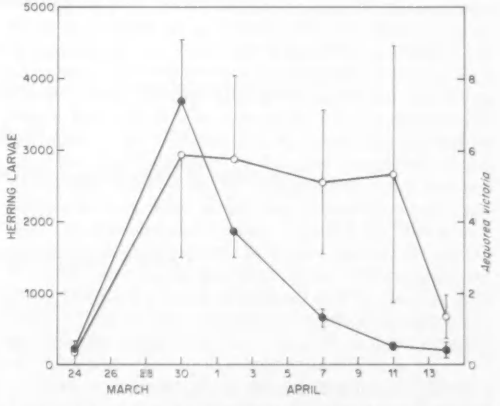

FIG. 3. Numbers of herring larvae (closed circles) and *Aequorea victoria* (open circles), Baynes Sound, spring 1981; numbers per 32 m^3 haul averaged for nine stations; vertical lines indicate standard error.

Columbia waters only much later than the peak abundance of herring larvae.

Although we have no data on actual feeding rates, it is interesting to speculate on the effect medusae could have on the herring larvae population in bays such as Baynes Sound. For example, 10 *Aequorea victoria* initially 1.4–2.0 cm were grown in the laboratory on a diet of *Pleurobrachia* for 28 d (Arai 1980). They used an average of 8.0 mg ash-free dry weight of *Pleurobrachia* per day. Herring larvae average approximately 0.14 mg ash-free dry weight (Duenas 1981), i.e. an equivalent diet of herring larvae would comprise 57 larvae per day. If the ratio of *Aequorea* to herring larvae was 1:625, the *Aequorea* could be taking 9% of the herring daily during the peak of larval abundance in Baynes Sound. Even assuming that the vagaries of field contact and the presence of alternative prey reduce the larvae caught to a tenth of this calculated figure, this would lead to a conservative estimate of *Aequorea* predation in Baynes Sound of 0.9% of the herring daily.

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A Multilocus Genetic Model Applied to the Effects of Selective Fishing on the Growth Rate of Trout

L. D. FAVRO AND P. K. KUO

Department of Physics, Wayne State University, Detroit, MI 48202, USA

J. F. MCDONALD

Department of Mathematics, University of Windsor, Windsor, Ont. N9B 3P4

D. D. FAVRO

Roeper School, Bloomfield Hills, MI 48013, USA

AND A. D. KUO

Athens High School, Troy, MI 48098, USA

FAVRO, L. D., P. K. KUO, J. F. MCDONALD, D. D. FAVRO, AND A. D. KUO. 1982. A multilocus genetic model applied to the effects of selective fishing on the growth rate of trout. Can. J. Fish. Aquat. Sci. 39: 1540–1543.

We used a generalized genetic model with varying numbers of genes to investigate the effects of selective fishing on the growth rate of trout. Our results indicate that the effects are not highly dependent on the details of the genetic model. In particular, the size distribution of the population in the long run seems to be insensitive to the number of active loci which control the growth rate of the fish.

Key words: fish, trout, genetics, growth, size limit, population

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Un modèle génétique généralisé avec nombres variables de gènes a servi dans l'étude des effets d'une pêche sélective sur le taux de croissance de la truite. Les résultats indiquent que ces effets ne dépendent pas étroitement des détails du modèle. En particulier, la distribution des tailles dans la population semble insensible à long terme au nombre de loci actifs contrôlant le taux de croissance des poissons.

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PREVIOUS work (Favro et al. 1979, 1980) has demonstrated that it is possible for a mathematical population-genetic model to describe size-distribution changes in populations of wild trout which are subject to selective fishing. In that work, a particular two-locus model reproduced the detailed structure of size-distribution changes in the AuSable River of Michigan over a 20-yr period. However, serious questions can be raised as to whether the close agreement between the predicted and observed changes are characteristic of the genetic process itself or are the result of a fortuitous choice of the particular structure of the genetic model which was used in that work.

Here we present the results of similar calculations done with a much more general model in which the genetic structure has a large degree of flexibility. While the development of this model was primarily motivated by the need to test the structure-dependence of the previous results, the use of this model is by no means limited to that purpose. It is in fact capable of calculating the effects of any given selection process (or processes) when the selected trait (or traits) is controlled by as few as one pair of genes or as many as four pairs of genes.

In particular, this new model incorporates four independent loci with two possible alleles at each locus. Linkages, if desired, may be easily included. Like the previous model, this model has been specifically designed for fisheries work by incorporating a generalized growth curve with seasonal variations in the growth rate, and by making the fecundity of females dependent on their weight. Our specific use of the model here is to calculate the effects of length-dependent selective fishing (sport fishing) on hypothetical populations in which the growth rate of the fish is genetically controlled, and to test the sensitivity of the results to variations in the number of genes involved.

The organization of the population calculation in the computer program is reflected in the block diagram of Fig. 1. An initial distribution of ages and genotypes together with information about growth, natural mortality, and fishing pressure (all as a function of time) are used as input data. In the block marked "Advance One Year" the program combines these data on a weekly basis to calculate net growth and mortality for the year. Gamete production is then calculated on the basis of the fall population numbers with the fecundity of females taken to be proportional to their weight which in turn is taken to be proportional to the cube of their length. All year-classes except the first two are allowed to contribute to the total gamete pool so that back-crossing occurs with all previous generations. These gamete numbers are combined randomly (i.e. the random mating hypothesis is assumed) to find the distribution of gametotypes in the new generation. The overall number of offspring is adjusted to be exactly equal to the number of fish removed from the population during the previous year so that the total population does not vary from year to year. The computer then recycles with the newly calculated population replacing the initial population of the previous year. The computer keeps track of the genetic makeup and populations of each generation until age 15, and size distributions are printed out at specified times, usually at 5-yr intervals.

Input data for the program — To use the computer program we must supply it with growth and mortality information and with some initial distribution of ages and genotypes. The growth rate of the fish in our model follows the growth formula of Favro et al. (1979) modified to include seasonal variations as in Favro et al. (1980). Different phenotypes are distinguished in this formula by a parameter S_F (called $S_\mu(\infty)$ in our previous work) which is essentially the average asymptotic length that would be attained by fish of that type if they were to live forever. The value of S_F for each phenotype is determined in the following way. At each of the four loci we allow two possible alleles, one that causes an increase in the growth rate, denoted say by a capital letter, and one that causes a decrease in the growth rate, denoted by a lower case letter. We then assign a number, F, called the "fast growth gene count" to each genotype by simply counting the number of capital letters in the genetic designation of the genotype. Thus, *AABbCcDD* would be assigned an F of six, etc. With four loci there are then nine possible phenotypes corresponding to values of F ranging from 0 to 8. With three loci there are seven phenotypes with F ranging from 0 to 6, etc.

The asymptotic size, S_F, is taken to be a linear function of F, i.e. $S_F = \alpha + \beta F$. The values of S_F then range from α to $\alpha + 8\beta$ with four loci, from α to $\alpha + 6\beta$ with three loci, etc. Since we wish to compare the results of calculations done with different numbers of loci, the values of α and β are chosen to satisfy two conditions. First, the mean value of S_F should be 50 cm for each number of loci[1]. (This value was chosen because it is the same as the value in the previous model.) Second, the width of the distribution of values of S_F, measured by the standard deviation from the mean 50-cm size

[1]The actual mean size of fish in the population is of course very much smaller than this value since few, if any, fish live long enough to approach their ultimate sizes.

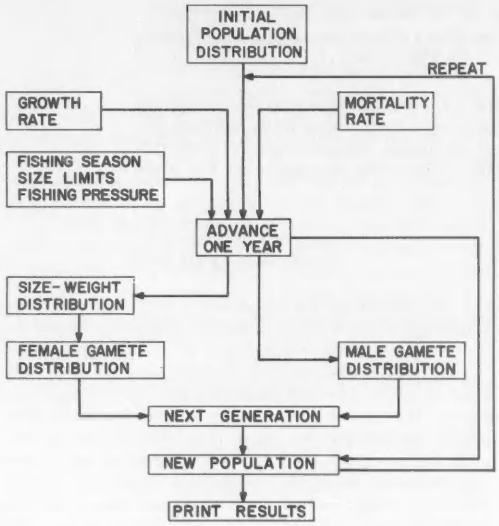

FIG. 1. Block diagram of the computer model.

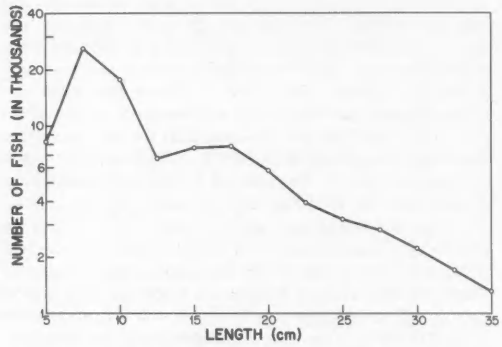

FIG. 2. Initial size distribution for the present computer model when there are three active genes that control the growth rate.

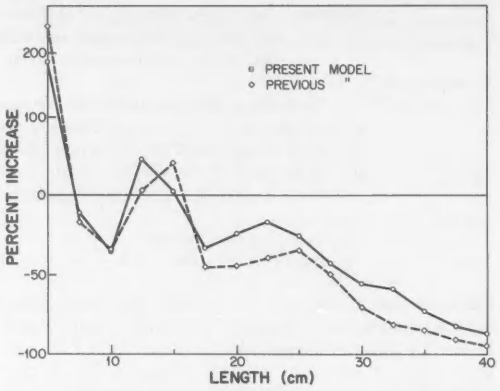

FIG. 3. Comparison of the percentage changes in the population over a 20-yr period computed with the present model and the previous model of Favro et al. (1979).

TABLE 1. The percentage changes in the population numbers versus size over a 20-yr period for various numbers of active loci. The lengths given are in centimetres and denote the center of an interval of length 2.5 cm.

Length (cm)	2 Loci	3 Loci	4 Loci
5.0	191.9	209.4	215.4
7.5	−11.2	−4.4	−1.9
10.0	−35.6	−41.3	−41.7
12.5	46.4	47.0	44.4
15.0	4.9	5.7	8.6
17.5	−33.1	−27.1	−26.8
20.0	−24.3	−29.4	−27.7
22.5	−17.1	−17.3	−17.8
25.0	−25.9	−26.8	−26.8
27.5	−42.6	−40.4	−41.7
30.0	−55.8	−57.1	−57.0
32.5	−59.4	−63.5	−65.8
35.0	−73.0	−73.5	−74.5
37.5	−82.5	−82.1	−82.1
40.0	−86.8	−88.1	−88.2
42.5	−92.1	−92.5	−92.2
45.0	−95.7	−95.2	−95.0
47.5	−97.5	−97.3	−97.0
50.0	−98.5	−98.4	−98.2

for a random distribution of genotypes, should be the same in all cases. Again, the value of this standard deviation was taken to agree with the previous model to facilitate comparison with that model. The resulting values of α and β for two loci are 32.3 and 8.8 cm; for three loci 28.3 and 7.2 cm; for four loci 25.0 and 6.3 cm.

In the previous model the yearly survival rate for fish outside the legal size range was taken to be a constant, e^{-a}, chosen to agree with Michigan Department of Natural Resources (DNR) mortality data, and for fish within the legal size range a different, genetically dependent constant, $e^{-a-b\mu}$ was used. The term $b\mu$ was chosen to represent the additional mortality due to fishing pressure. The parameter μ characterized the genetic makeup of the fish and was introduced there to represent the fact that mortality will be higher for faster-growing fish because of their greater feeding activity. It may be omitted if desired (Favro et al. 1980). The constant b is adjusted to give some preassigned average additional mortality due to fishing or may be considered to be an adjustable parameter which is used to fit data. Since the growth rate in the present model depends on the parameter F and not μ, and since the number of growth-rate phenotypes depends on the number of loci involved, a somewhat modified form of the mortality rate is used here. For fish outside the legal range, the same form, e^{-a}, is assumed. For fish within the legal range, the parameter F replaces μ in the exponent and, in addition, the constant b which describes the fishing mortality rate is

chosen differently for different numbers of loci. The values of b which are used are determined by the formula

$$b = -\ln[1 - (e^a - 1)P]/m.$$

Here m is the number of loci and a is the parameter defined above to specify the natural mortality rate. The parameter P is the same as the fishing pressure parameter defined in Favro et al. (1979). It is essentially the additional mortality rate due to fishing expressed as a fraction of the natural rate. This rather complicated-looking form for b makes the additional instantaneous mortality rate due to fishing pressure, when averaged over a random distribution of genotypes, independent of the number of loci m. In addition, it makes the additional *yearly* mortality exactly the specified fraction P for any value of m. These features of the mortality rate are mandated by our desire to compare calculations with different number of loci on an equal basis.

Our initial population is normally taken to consist of a Hardy–Weinberg distribution of genotypes with an age distribution which corresponds to the natural mortality rate with no fishing pressure. For the purpose of this work, which is to compare genetic models in which the growth rate of the fish is controlled by different numbers of loci, we have assumed that all alleles occur with equal probability in the initial population. Since the calculated results are quite insensitive to the initial allele distribution as long as it is not made grossly asymmetrical this assumption is not critical. However, it does have the effect of giving the best possible fit between the initial size distributions with different numbers of loci. A plot of the initial size distribution for the three-locus model is given in Fig. 2. The size distributions for the two- and four-locus models differ so little from this curve that it is not feasible to superimpose them on the graph. All three distributions exhibit all the usual features of natural population size distributions: well-defined peaks due to the first two year-classes, a nearly exponential decrease in the larger size range, etc. Each of the distributions is stable under the combined effects of natural mortality (with no selection process included) and reproduction as represented in the genetic programs described.

Results — To test the sensitivity of the results of Favro et al. (1979 and 1980) to the details of the genetic structure, we have used the present model with its parameters adjusted to give the same growth rate, mortality, etc. in all cases to calculate the percentage changes in the population size distributions when selective fishing is present. The initial population was taken to be the Hardy–Weinberg distribution described above and the changes were calculated over a 20-yr period. The mortality of legal size fish during the fishing season was taken to be 40% higher than the natural mortality rate. This value was chosen because it was the one needed in Favro et al. (1979) to fit the observed changes in the population of *Salmo trutta* in the AuSable River of Michigan during the period from 1959 to 1977.

A comparison of the genetically induced size distribution changes in the present model with the model of Favro et al. (1980) is given in Fig. 3. The results are given as percentage changes from the initial distributions, Fig. 2, over a 20-yr period with the legal size limit for fishing set at 25 cm. While the actual plot for the present model represents only the two-locus version of the model, the plots for the three-locus and four-locus versions would yield the same comparison because they do not differ in any significant way (see Table 1). The two models are seen to be in quite good agreement in their general behavior over the whole range plotted both in regard to their characteristic shape and in regard to the magnitude of the population changes. The differences that do appear are attributable to minor differences in the average growth rates, initial population distributions, etc. caused by the different methods of assigning phenotypes in the two models. These differences could easily be compensated by relatively minor changes in the parameters, e.g. the fishing pressure parameter P (see Favro et al. (1979), fig. 5), of either model. In any case, the curves for the two models are indistinguishable on the scale of the observational errors in the data plotted in Favro et al. (1979).

A detailed comparison of the effects of changing the number of active loci within the same model is difficult to accomplish graphically because the differences among them are so small that the various curves overlap. The actual numerical values of the percentage changes of each population size from the initial values over a 20-yr period are given in Table 1. These values show that the results are almost totally insensitive to changes in the number of active loci. This insensitivity to the number of loci, combined with the insensitivity of the results to the change in the size-phenotype assignments contained in the changes from the model of Favro et al. (1979), indicate that the salient features of the calculated population changes are characteristic of the genetic process itself. We then must conclude that the agreement between the observed population changes and the calculations of Favro et al. (1979) is not an accidental result of the choice of model. In view of the statistical uncertainty in observed population numbers and the uncertainty in our knowledge of the mortality rate attributable to fishing it would be extremely difficult to distinguish among differing genetic models on the bases of changes in the observed size distribution alone. Further evaluation of the model must await the accumulation of more precise data on population sizes or perhaps direct genetic experimentation with fish taken from the wild.

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Comment on Electroencephalographic Responses to Morpholine and their Relationship to Homing

COMMENT

I would like to address questions about electroencephalographic (EEG) responses to morpholine and their relationship to homing which have been raised in Hara and Brown (1979). These questions were originally examined in depth in Cooper and Hirsch (1982), but because the editor rewrote the passages of the chapter without our consent, the precise nature of our criticism of Hara and Brown (1979) was lost and the meaning was changed. Herein I will present our original criticism and discuss Hara and Brown's findings in light of our own work. The three areas of concern are (1) imprinting, (2) homing, and (3) olfaction.

Although the studies of Hara and Brown undertake "to characterize further the nature of the electrical responses included in the olfactory bulb by nasal infusion of morpholine" they imply that they can clarify the role of the EEG in studying homing, artificial imprinting, or the use of olfaction in homing. Their studies cannot help in this regard.

In contrast to the usefulness of the EEG as a correlate to artificial imprinting experiments (Cooper and Hasler 1976), the technique appears to be of only limited value for studying homing (Bodznik 1975; Cooper 1974). Non-home water samples have occasionally elicited stronger responses than home water (Oshima et al. 1969; Dizon et al. 1973; Bodznik 1975). Bodznik (1975) found no relationship between the relative EEG responses of the fish to the homestream waters and the actual behavioral response of the fish to the same water during migration. The relative EEG responses to the natural waters appeared to change during the spawning migration within a population of fish. In addition, other factors such as temperature of the test water, pH, electrode type and position, and length of time that fish were held before experiments make the results hard to interpret.

Our EEG experiments (Cooper and Hasler 1976) provide evidence leading to the conclusion that previous exposure to morpholine (at an extremely low concentration) significantly influences the subsequent electrical responses recorded from the olfactory bulb. This is the main point of our experiments. The EEG responses may be a mechanism of the central nervous system for memory recall or only a correlate that happens to simulate quite closely the observed behavior of the animal. It is evidence of olfactory imprinting, even though the EEG responses may be through some other sensory system. This experiment has been performed on four paired groups of 90 coho salmon as well as one paired group of migratory rainbow trout over a period of 2 years, so that results are consistent (Cooper and Hasler 1974). Dizon et al. (1973) obtained similar results. At least one independent reviewer has accepted this conclusion (Leggett 1977).

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The first major problem with the experiments of Hara and Brown is that they never demonstrated that their fish were imprinted to morpholine. The EEG technique is only a useful *correlate* of olfactory imprinting; one can learn little about imprinting using this technique unless one is sure that one's fish have been imprinted — as could be demonstrated by behavioral or other experiments. Since there is no evidence to suggest that the fish used by Hara and Brown were imprinted, one can draw no conclusions about the nature of the EEG responses to an imprinted substance (which was morpholine in our experiments). In fact many responses seen in the experiment of Hara and Brown might be expected from non-imprinted fish (see below).

Two features of the experiments by Hara and Brown may explain their inability to imprint trout in their experiments. The rainbow trout available to these researchers were a non-migratory group that have not been shown to behave in a manner similar to the migratory rainbow or "steelhead" trout. The nonmigratory trout may simply not imprint in the same manner as migratory fish.

A second reason that the experiments of Hara and Brown (1979) may not be useful in understanding homing is the hormonal condition of the trout. The fish in their experiments were not in spawning condition and thus hormonal balances were different from those of homing salmonids (Scholz 1980). In an earlier paper (Cooper and Hasler 1973), it was postulated that as hormonal titers increased, long-term memory components such as a possible olfactory memory might be selectively recalled (possibly even at the expense of "short-term" memory items such as food, location of feeding grounds, or the identification of predators). There is a large body of information that indicates that salmonids in spawning condition respond differently than nonspawning fish including changes in olfactory thresholds (Kleerekoper 1969). Thus it is inappropriate for Hara and Brown (1979) to study homing with nonmigratory, nonspawning trout.

Setting implications about homing aside, there still appear to be problems with the attempts of Hara and Brown (1979), Hara and Macdonald (1975) and Hara (1974) to characterize the EEG response to morpholine. There are large inconsistencies in their results which are not explained. Hara (1974) and Hara and Macdonald (1975) had to repeat the application of 1% morpholine to elicit strong responses from nonmigratory, sexually immature rainbow trout. By contrast Hara and Brown (1979) report that all experimental fish (in nonspawning condition) responded with high intensity to 1% morpholine. In earlier experiments Hara (1974) and Hara and Macdonald (1975) indicate that there was an inhibition in the background EEG activity at 0.1 and 0.01% morpholine, while Hara and Brown (1979) report strong responses near these concentrations. Thus these researchers do not appear to be getting consistent results with which to compare the experiment of Cooper and Hasler (1974).

The responses to morpholine in the present experiments were characteristic of what one might expect from non-imprinted fish. There were no significant differences between responses of the experimental and control fish in the experiments of Hara and Brown (1979). The high intensity responses to 1% morpholine reported were essentially identical to those responses seen in the experiments of Cooper and Hasler for imprinted salmon or trout to 1% morpholine. The major difference is that *nonimprinted* fish in our experiments did *not* respond (or responded weakly) to 1% morpholine. Thus it appears that in spawning condition only imprinted fish would respond to morpholine, the appropriate homing cue in our experiments. It is difficult to imagine that such a response could come through "a nonspecific irritational effect at non specialized cell surfaces," as hypothesized by Hara and Brown.

Cooper and Hasler (1974) have often acknowledged that the responses to morpholine are qualitatively different from responses to other substances by morpholine-imprinted fish (Cooper and Hasler 1974, 1976; Cooper 1974). It should not be assumed, however, that there are no differences qualitatively to other substances, since this has been observed (Cooper 1974). Thus the description of EEG signal responses to morpholine (Hara and Brown 1979) support rather than refute previous research and is not evidence that EEG responses to morpholine are nonolfactory.

Cooper and Hasler (1974) do assume that morpholine is detected by olfaction. If responses were due to pH or some other general irritant effect (Hara 1974; Hara and Macdonald 1975; Hara and Brown 1979), then one might expect no difference in responses between imprinted and control fish. As reported there were highly significant differences in responses to morpholine for these two groups. As discussed above the failure to find a difference in the responses of the two groups in the experiments of Hara and Brown cannot speak to the question of imprinting since their experiments lack the evidence that the experimental group was imprinted. Experiments by Hirsch (1977) also support responses by olfaction. However, the need to use high concentrations of morpholine in EEG experiments may indicate that this technique is making use of a sensory system which is responding in close correlation to the olfactory system rather than olfaction per se.

The suggestion of Hara and Brown that the "sensitization due to imprinting may not be detectable by simple comparisons of the bulbar responses to morpholine with those of a standard substance (NaCl or amino acids), because the salmon should have been imprinted *differently* [my underline] to the standard substances as well," is not supported by our data (Cooper and Hasler 1976). The responses to NaCl and l-methionine were examined (using each, alternately, as a "standard" for the other) and no significant differences in responses from the imprinted and nonimprinted groups of salmon were found. Furthermore the water source at the fish hatchery in our imprinting experiments was identical for both experimental and control groups of fish.

Hara and Brown (1979) found perfusion of 1% morpholine into the nares for 10 min irreversibly inhibited the EEG response to l-serine. This was given as a basis that "non-specific irrational" instead of olfactory responses were responsible for EEG response to morpholine in the experiment of Cooper and Hasler (1979). This point does not follow since many substances might eliminate olfactory responses if they were used for perfusion at such large doses.

Although ablation studies are needed to resolve whether morpholine is detected by olfaction, there is ample behavioral evidence that olfaction is important in this system. Morpholine is detected at very low concentrations both in a laboratory study (Wisby 1952) and field research (Madison et al. 1973; Scholz et al. 1973). A concentration of 5×10^{-5} mg/L is sufficient for imprinting juvenile coho salmon and rainbow trout and for decoying these fish to a stream scented with morpholine. Since no other sensory system is known to operate at such low concentrations, olfaction is considered to be the sensory modality. Recent research (Tucker 1973; B. Oakley personal communication) indicates that gustatory systems of some fish are extremely sensitive. This system should also be considered in this case, although high sensitivity of the gustatory system has not been demonstrated for salmonids. Neither have gustatory receptors been reported in the nares.

Results offered with the EEG technique are in close agreement with other parts of artificial imprinting studies (Cooper et al. 1976; Scholz et al. 1973). We conclude that coho salmon and rainbow trout can imprint to morpholine, retain this information until the spawning migration, and use it to identify a stream scented with this chemical. The response to this odor is specific in that a compound similar to morpholine (N-B-hydroxyethylenemorpholine) and another organic chemical odor (phenethyl alcohol) failed to elicit responses. These data provide support for the olfactory hypothesis: salmon may imprint to morpholine in the same way as they do to naturally occurring homestream odors. — JON COOPER, *U.S. Environmental Protection Agency, HERD (TS-796), 401 M St., S.W. Washington, D.C. 20460, USA.*

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REPLY

Cooper is incorrect in stating that "they [Hara and Brown] imply that they can clarify the role of the EEG in studying homing, artificial imprinting or the use of olfaction in homing." The objective of a series of electrophysiological investigations we conducted was to characterize the olfactory bulbar responses induced by nasal infusion of morpholine, and no attempt was made to evaluate homing by trout exposed to morpholine (Hara 1974; Hara and Macdonald 1975; Hara and Brown 1979). We question the validity of electrophysiological analyses of the olfactory bulbar responses in salmonids imprinted to morpholine.

The electroencephalographic (EEG) responses, or more accurately induced waves (Adrian 1950) of the olfactory bulb due to nasal infusion of chemical stimuli are rhythmic, oscillatory potentials, and are believed to be the result of synchronous activity of the secondary neurons within the olfactory bulb. Typically, upon introduction of a stimulus into the nares, the spontaneous activity of the bulb is *immediately interrupted by oscillatory waves that are terminated on cessation of the stimulus*. Although there is a close correlation between the bulbar response and the electro-olfactogram (EOG) responses of the olfactory mucosa, the nature of the induced waves is not yet fully understood. However, it is generally accepted in olfactory physiology that the bulbar induced waves are to be used only to monitor the responsiveness of the olfactory system of an animal to odor stimuli, and not to be used for analyzing mechanisms of the central nervous system functions such as odor discrimination, memory and so on. This does not, therefore, support Cooper's view that "the EEG responses may be a mechanism of the central nervous system for memory recall or only a correlate that happens to simulate quite closely the observed behavior of the animal ..... The EEG technique is only a useful *correlate* of olfactory imprinting, ..."

Contrary to Cooper's claim, our results have been highly reproducible and consistent in that:

1) All the fish we tested respond to 1.1×10^{-1} mol/L (1%) morpholine with high intensity, and to a greater extent with successive stimulus application.
2) Mopholine at 1.1×10^{-2} mol/L and 1.1×10^{-3} mol/L (0.1 and 0.01%, respectively) inhibits the background bulbar activity without positive response (see Fig. 1 and 2, Hara and Brown 1979).

This consistency in data has been achieved by the use of a highly controlled, reliable stimulant delivery system developed in our laboratory (Hara et al. 1973). The stimulatory apparatus consists of three-way valves operated by pneumatic actuators, solenoid valves and an electronic time switch. This contrasts with an uncontrolled, unreliable method of stimulus application employed by Cooper's group, where from 6 to 10 mL of stimulant at an approximate rate of 1 mL/s was delivered via a wash bottle, cannulae or Pasteur pipette (Scholz et al. 1973; Cooper 1974; Cooper and Hasler 1974). This kind of constancy in stimulus application is especially required when the bulbar responses are quantified by means of a DC integrator (Cooper 1974), where the slope is largely influenced by an initial rate of stimulus impingement.

For the reason discussed in Hara (1974) and Hara and Macdonald (1975) and reiterated in Hara and Brown (1979), the effects of 1.1×10^{-1} mol/L morpholine on our fish stocks appears to be nonspecific and irritational. The basis for this conclusion is derived from several factors concerning the characteristics of the bulbar response to morpholine and its effect on other olfactory substances. *Morpholine induces a large, long-delayed and long-lasting response which is not readily terminated upon rinsing*. This response is distinct and atypical when compared to the responses induced by odorants such as food extract, hand rinse, mucous substances and amino acids (Hara 1975, 1982). A solution of 1.1×10^{-1} mol/L morpholine, a strong base, has a pH greater than 10, and a large part of the morpholine response disappears when the pH is reduced. Indeed, Cooper and Hasler (1974, 1976) found no responses to buffered morpholine solutions. Thus, morpholine is effective only at adverse environmental pHs.

Application of 1.1×10^{-1} mol/L morpholine into the nares for 10 s inhibits, after rinsing, subsequent responses to L-serine (Hara 1974; Hara and Macdonald 1975). Exposure to 1.1×10^{-1} mol/L morpholine for longer periods *irreversibly* inhibits responses to L-serine (Fig. 5 of Hara and Brown 1979). This is different from *temporary* inhibition due to the sensory adaption Cooper pointed out. To search for olfactory specificity using 1.1×10^{-1} mol/L morpholine as stimulus is like trying to determine the gustatory threshold for acid by using a 1% (0.27 mol/L) HCl solution as stimulus.

Aside from the differences in maturity and migratory condition of our fish pointed out by Cooper there are several other important differences between our investigations and those by Cooper and Hasler (1974, 1976). The difference relates to the

use of 6×10^{-2} mol/L NaCl as a standard stimulus. Cooper (1974) reported that 6×10^{-2} mol/L NaCl serves to hold the background constant and in the majority of cases produced no response by itself. This type of standard (essentially background activity) does not account for differences in responses between groups or individuals which are inherently different for reasons other than morpholine treatment. A close examination of data presented by Cooper and Hasler (1974, 1976) suggests that it may be necessary to account for inherent differences in sensitivity. Cooper and Hasler (1974) noted that morpholine-exposed salmon showed an increasing responsiveness to buffer during the season. Data from Cooper and Hasler (1976) also exhibited changing responsiveness because the responses to 1.7×10^{-1} mol/L NaCl appeared to decrease after November 1 (Fig. 14 in Cooper 1974). Cooper and Hasler (1976) used methionine compared to the 6×10^{-2} mol/L NaCl standard to test for differences in responsiveness between morpholine-treated and control groups. They found no difference for fish from experiments 2a and 2b; however, morpholine-exposed coho salmon from experiment 2c were more responsive to methionine as well as morpholine. Would methionine not be a better standard for these experiments? When coho data from Cooper and Hasler (1976) were analyzed using methionine as standard, only experiments 2b showed significant differences between morpholine-exposed and unexposed fish (Cooper 1974). (Note that the use of methionine would be similar to our using L-serine as standard). Similarly, if the values found for 1.7×10^{-1} mol/L NaCl (a concentration which generally elicited a response greater than background) is used as standard, only the results from experiment 2c show differences by the Mann–Whitney U-test. If the few fish that do not respond to 1.7×10^{-1} mol/L NaCl are eliminated then none of the three experiments show differences. Responses to methionine or 1.7×10^{-1} mol/L NaCl were not given in Cooper and Hasler (1974). However, if the response to the buffer solution is used as standard then there is no difference between morpholine exposed and control individuals.

The changing responsiveness of the salmon to 1.7×10^{-1} mol/L NaCl before and after November 7 raised a second question, involving the use of a ranking procedure to evaluate the differences between the groups tested. The morpholine-exposed fish outnumbered the unexposed fish 20 to 11 at a time when the fish appeared generally more sensitive to chemical stimulation. In contrast, after November 7 the ratio of the treated to control fish was 19 to 20. Would the higher numbers of treated fish captured and tested at a time when the fish were more responsive probably contribute more higher ranks and result in differences that may not actually be present?

Although behaviorally we did not demonstrate that our fish were imprinted, we still feel that sensitization due to imprinting may not be detectable by simple comparisons of the bulbar responses to morpholine with those to a standard substance. Amino acids and inorganic ions are ubiquitous and present in natural waters at concentrations that could be detected by fish (Burnison 1971). Could fish not imprint to these chemicals as well? After all, fish do not live in distilled water scented with morpholine alone. Findings by Cooper and Hasler (1976) do not invalidate this suggestion, especially considering that when methionine or 1.7×10^{-1} mol/L NaCl is used as a standard in their investigation fewer differences are apparent.

Homing of salmonids artificially imprinted to a low level of morpholine is evident from extensive behavioral studies (cf. Hasler et al. 1978). However, the involvement of olfaction in imprinting to morpholine at 5.7×10^{-10} mol/L has not been adequately established. Using electrophysiological experiments, no homing coho salmon responded to morpholine lower than 1.1×10^{-2} mol/L (Cooper and Hasler 1974, 1976). In our studies, morpholine produced no olfactory response before the concentration reached 10^{-3} mol/L where it rather caused inhibition of background electrical activity. Recent heart rate conditioning studies by Hirsch (1977) show that coho salmon were not able to detect morpholine at concentrations lower than 2.3×10^{-8} mol/L. However, the sensitivity does begin to approach that required to detect morpholine at imprinting and decoying concentrations. This does not mean that fish are unable to detect the chemical. Electrophysiological and cardiac conditioning techniques may not be sensitive enough to record a response, or alternatively chemical imprinting and homing may have occurred via sensory channels other than olfaction. Gustatory systems in fish are as sensitive to chemical stimulation as olfactory (Caprio 1982). Salmonids in particular are highly sensitive to certain taste stimuli (Marui and Hara, unpublished). Cauterization studies are necessary to resolve whether the behavioral responses attributed to morpholine are mediated via olfaction. — TOSHIAKI J. HARA AND S. B. BROWN, *Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Man. R3T 2N6.*

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OBITUARY / NÉCROLOGIE

Professor Michitaka Uda
1905-1982

Professor Uda was well-known to most Canadian oceanographers. His series of lectures given at the Pacific Oceanographic Group, Nanaimo (Uda 1959) served as a basic introduction to the subject of fisheries oceanography — a subject that the Japanese considered important 20 years ago and one which we are now only beginning to recognize in Canada. Professor Uda's subsequent description of the oceanography of the Subarctic Pacific Ocean (Uda 1963) was a landmark publication at its time in the history of Canadian oceanography. His primary mission in advancing the interdisciplinary nature of oceanography was recognized throughout the world. A fitting tribute to his many international activities was the dedication of the book, *Oceanic Fronts in Coastal Processes* (1978), "To Michitaka Uda." He published over 350 papers and books on oceanography.

Professor Uda's humour and joviality were as well-known as his science. His mastery of a form of pidgin English was as much a delight to the listener as it was to himself. His expressions of friendliness transcended the spoken word. His ability as a "Haiku" poet was well-known to his Japanese colleagues, including the Emperor in front of whom he was invited to recite his poems.

Professor Uda was a graduate of Tokyo Imperial University where he received his B.Sc. in 1927 and his Ph.D. in physics in 1939. He was director of the Nagasaki Meteorological Observatory from 1947 to 1949, and director of the Tokai Regional Fisheries Laboratory, 1949–51. Professor Uda survived the Hiroshima atomic bomb attack; his death in Tokyo was due to cancer. He is survived by his wife, two sons and one daughter.

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T. R. PARSONS
Department of Oceanography
University of British Columbia
Vancouver, B.C. V6T 1W5

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Books Received/Livres reçus[1]

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Coastal Research in the Gulf of Bothnia. *Edited by Karl Müller. Monographiae Biologicae 45. Dr. W. Junk Publishers. The Hague–Boston–London. 1982. xiv + 462 p. Dfl. 200, $87. (U.S.).* The Gulf of Bothnia is an unique region for brackish water research and this book concerns the interactions between a coastal stream and the adjacent coastal areas and the sea. Organisms living in the area have adapted to changes in water chemistry, especially salinity. Twenty-nine members of the staff at the University of Umeå present here the results of the first ecological survey of the Gulf. [R442]

Ecology of Coastal Waters: a Systems Approach. *K. H. Mann. Studies in Ecology Volume 8. University of California Press. Berkeley and Los Angeles. 1982. x + 322 p. $36 (cloth), $18 (paperback).* The approach in this book is on ecological processes rather than on organisms or populations. Thus primary production, grazing, predation, secondary production, detritus formation, decomposition, energy flow, nutrient cycling, etc. are the topics covered. The author concentrates on recent work; he enunciates principles involved and gives key references. [R443]

Fish By-Catch. . .Bonus from the Sea. *Report of a Technical Consultation on Shrimp By-Catch Utilization held in Georgetown, Guyana, 27–30 October 1981. Published by the International Development Research Centre under special arrangement with the Food and Agriculture Organization of the United Nations. 1982. 163 p. $15.* The purpose of the technical consultation was to prepare and start implementing a comprehensive and coordinated global action program aimed at the full use of the by-catch (fish unintentionally caught by vessels and thrown away at sea) from shrimp-fishing activities. [R444]

Seminario Regional sobre Recursos Demersales y su Medio Ambiente en el Pacifico Oriental. Lima Perú, 24–28 de noviembre de 1980. *Comision Permanente del Pacifico Sur (CPPS), Serie Seminarias y Estudios 3, Lima, Perú (Nueva direccion Quito, Ecuador). 1981. 260 p.* In Spanish. Includes papers from a regional conference on the demersal resources and their normal habitats in the south Pacific. [R445]

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[1]Persons interested in reviewing books in this list should contact the Book Review Editor, Canadian Journal of Fisheries and Aquatic Sciences, Scientific Information and Publications Branch, Department of Fisheries and Oceans, Ottawa Canada K1A 0E6.

[1]Les personnes intéressées à examiner les livres énumérés dans cette liste sont priées de communiquer avec le Rédacteur des comptes rendus, Journal canadien des sciences halieutiques et aquatiques, Direction de l'information et des publications scientifiques, Ottawa Canada K1A 0E6.

ANNOUNCEMENTS/AVIS

Symposium on Integration of Ecological Aspects in Coastal Engineering Projects

The Rijkswaterstaat of the Dutch Ministry of Transport and Public Works has organized this symposium, which is co-sponsored by UNESCO, IAWPRC, and IAHR, to be held in Rotterdam, Netherlands, from June 6–10, 1983. Participation by anyone interested in environmental and hydraulic coastal engineering projects is encouraged. Ecologists trying to promote application of their findings outside their own specific field, civic engineers involved in consequences of coastal hydraulic engineering projects, regional planners concerned with environmental plans for these particular areas, and administrators or managers involved in the decision-making process concerning coastal structures and influenced areas are especially invited.

The invited case papers will deal with protective measures planned for the lagoon of Venice, Italy; tidal power plans for the Canadian Bay of Fundy and the English Severn Estuary; the barrage plans for the Nakdong River in South Korea; the protective measures and land reclamation in the former Zuider Zee in the Netherlands; and the final phase of the protective project under construction in the Delta area of the Netherlands. Contributed papers will also be presented. The official language of the Symposium will be English.

For further information please contact: *Mr R. de Vlugt, Secretary of the Symposium organizing committee, Delft Hydraulics Laboratory Public Relations Department, P.O. Box 177, 2600 MH Delft, Netherlands. Telex: 38176 hydel-N1; Telephone: 015-569353.*

Colloque sur l'intégration des aspects écologiques de projets d'ingénierie côtiers

Ce colloque est organisé par le Rijkswaterstaat du ministère hollandais du Transport et des Travaux publics, avec la participation de l'Unesco, de IAWPRC et de IAHR. Il se tiendra à Rotterdam (Pays-Bas) du 6 au 10 juin 1983. Toute personne intéressée aux projets d'ingénierie côtiers, environnementaux et hydrauliques est invitée à y participer. On invite tout spécialement les écologistes qui s'efforcent de promouvoir l'application de leurs découvertes en dehors de leur domaine propre, les ingénieurs civils impliqués dans les conséquences de projets d'ingénierie hydrauliques côtiers, les planificateurs régionaux oeuvrant dans ces domaines particuliers, et enfin les administrateurs ou les gestionnaires responsables des décisions relatives aux structures côtières et aux zones influencées par ces dernières.

Les communications sur des cas particuliers présentées par des personalités invitées traiteront des mesures de protection envisagées pour la lagune de Venise (Italie); des projets d'usines marémotrices de la baie de Fundy (Canada) et de l'estuaire anglais de la Severn; des plans de barrage pour le fleuve Nakdong (Corée du Sud); des mesures protectrices et réclamation des terres dans l'ancienne Zuider Zee des Pays-Bas; et la phase finale du projet de protection en voie de construction dans la zone du Delta des Pays-Bas. D'autres travaux seront également présentés. La langue officielle du colloque sera l'anglais.

Pour plus ample information, on est prié de communiquer avec : *Mr R. de Vlugt, Secretary of the Symposium organizing committee, Delft Hydraulics Laboratory Public Relations Department, P.O. Box 177, 2600 MH Delft, Netherlands. Telex : 38176 hydel-N1; Téléphone : 015-569353.*

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Effect of temperature on initial feeding in alevins of chinook salmon (*Oncorhynchus tshawytscha*) **T. A. Heming, J. E. McInerney, and D. F. Alderdice**

Cyclopoid predation on Lake Michigan fish larvae **J. H. Hartig, D. J. Jude, and M. S. Evans**

Factors controlling phytoplankton production in Lake Vanda (77°S) **W. F. Vincent and C. L. Vincent**

Predatory behavior and prey selectivity of the pelagic water mite *Piona constricta* **H. P. Riessen**

Stock definition in Atlantic herring (*Clupea harengus harengus*): genetic evidence for discrete fall and spring spawning populations **I. Kornfield, B. D. Sidell, and P. S. Gagnon**

Hepatic metallothionein in rainbow trout (*Salmo gairdneri*) as an indicator of metal pollution in the Campbell River system **M. Roch, J. A. McCarter, A. T. Matheson, M. J. R. Clark, and R. W. Olafson**

Susceptibility of trouts of different species and origins to various isolates of infectious pancreatic necrosis virus **A. Silim, M. A. S. Y. Elazhary, and A. Lagacé**

Macroinvertebrate colonization of multiplate samplers in the Ohio River: the effect of dams **D. C. Beckett and M. C. Miller**

Ingestion-limited growth of aquatic animals: the case for Blackman kinetics **R. E. Condrey**

The recent introduction of the seagrass *Zostera japonica* Aschers. and Graebn. to the Pacific Coast of North America **P. G. Harrison and R. E. Bigley**

Annual production by caddisflies and mayflies in a western Minnesota plains stream **M. B. MacFarlane and T. F. Waters**

Effects of copper on nitrogen fixation and growth of blue-green algae in natural plankton associations **W. A. Wurtsbaugh and A. J. Horne**

Comparison of searching behavior for zooplankton in an obligate planktivore, blueback herring (*Alosa aestivalis*) and a facultative planktivore, bluegill (*Lepomis machrochirus*) **J. Janssen**

Reproductive strategies in flatfish: a first synthesis **D. A. Roff**

Microbial ecology of the Bay of Fundy. I. Distribution and activity of attached and free-living suspended bacteria **L. M. Cammen and J. A. Walker**

Characteristics of sediment and organic carbon export from pristine boreal forest watersheds **R. J. Naiman**

Meristic variation in beaked redfishes, *Sebastes mentella* and *S. fasciatus*, in the Northwest Atlantic **I-H. Ni**

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Ichthyophthiriasis: immersion immunization of rainbow trout (*Salmo gairdneri*) using (*Tetrahymena thermophila*) as a protective immunogen **K. Wolf and M. E. Markiw**

Use of box and line plots to assess fish ventilatory behavior in biological monitoring systems **W. J. Sydor, W. R. Miller III, J. Cairns Jr., and D. Gruber**

Characteristics and identification of *Pasteurella* and *Vibrio* species pathogenic to fishes using API-20E (Analytab Products) multitube test strips **M. L. Kent**

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Volume 39, No. 11, November 1982 Volume 39, n° 11, novembre 1982

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Model of salmon age structure and its use in preseason forecasting and studies of marine survival **R. M. Peterman** 1444–1452

Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations **T. A. Dickson and H. R. MacCrimmon** 1453–1458

Release of methyl mercury from sediments: effects of mercury concentration, low temperature, and nutrient addition **D. R. Wright and R. D. Hamilton** 1459–1466

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Trophic upsurge in new reservoirs: a model for total phosphorus concentrations **Y. Grimard and H. G. Jones** 1473–1483

Descriptions and keys for ammocoetes of lampreys from British Columbia, Canada **J. E. Richards, R. J. Beamish, and F. W. H. Beamish** 1484–1495

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